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THE ORIGIN AND DEVELOPMENT OF THE EMBRYO SAC AND EMBRYO OF DENDROPHTHORA OPUNTIOIDES AND D. GRACILE. I[1]

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(WITH SIX FIGURES AND PLATES V AND VI)

Introduction

The Loranthaceae are parasitic plants that occupy a place of special interest among the dicotyledons. Since they are very peculiar, not only in their mode of life, but also in the structure of their reproductive organs, they have attracted much attention from plant morphologists. Although a considerable number of studies of the group have been made, their morphology and physiology are quite inadequately known. Our knowledge even of the European species of *Loranthus*, *Arceuthobium*, and *Viscum*, those that have been studied most, is as yet incomplete.

The Loranthaceae comprise more than 600 species and are confined largely to the tropics. Aside from the European species of the genera just mentioned, the development of these plants has been most fully studied in certain species of the same genera occurring in Java. In spite of the wide distribution of the genus *Phoradendron* in the southeastern United States and the occurrence of scores of other species in tropical America, comparatively little is known of the Loranthaceae of the Western Hemisphere.

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, no. 26.

The observations of the earlier writers on the reproductive organs of the Loranthaceae were concerned chiefly with the mature flowers and the development of the fruit. Their interpretation of the different floral organs and the relation of these to each other show that they had a very meager understanding of these structures. Nevertheless, some of these observations show considerable accuracy and are therefore worthy of mention.

WILLIAM GRIFFITH (**10**), in a paper read before the Linnaean Society of London in 1836, gave a brief description of the anatomy of the flowers and the development of the embryo in *Loranthus scurrula*. He asserted that the ovary is "intimately adherent" with the calyx and that some time after the "fall of the corolla a small cellular body appears attached at the base of the ovarian cavity." This structure, which is an elongation of the floral axis, he interpreted as the rudiment of an ovule, at the center of which, in later stages of development of the fruit, an embryo appeared. In a second paper read before this same society in 1843, GRIFFITH (**11**) described the mature embryo sacs of *Loranthus bicolor* and *Loranthus globosus*, stating that he believed they existed even before pollination. He found a "nipple-shaped process" at the base of the ovarian cavity and thought it might be a continuation of the floral axis. Not being sure of the homology of this process he limited his descriptions to the ovules, which he called embryo sacs, their relations to the pollen tubes, and the subsequent changes in them. His main conclusions are that the ovules in this genus are reduced to embryo sacs, and that "the embryo is a growth from the ends of the continuations of the pollen tubes, outside the anterior ends of the embryo sacs."

SCHLEIDEN (**31**) regarded the flowers of the Loranthaceae, which he studied in *Viscum album* and *Loranthus* sp., as the "simplest that can exist." He asserts that the two pairs of bracts of the perianth which bear the stamens are "metamorphosed into anthers" and the segments of the perianth in the carpellate flower "have the nature of a calyx." According to him the floral axis is prolonged between the sepals, forming a nucellus or "ovulum nudum." Furthermore, the tip of the nucellus constitutes a stigma, on which the pollen grains are deposited and into the tissue of which

the pollen tubes, containing the "germ of the embryo," grow downward to the embryo sacs, in which the embryos are nourished. He believed that the embryo sacs are formed in the "pith of the peduncle" or the center of the nucellus, and that the berry is to be regarded as a "metamorphosed peduncle." In conclusion, SCHLEIDEN states that "the Loranthaceae show, in a parasitic form, the intervening step between the Coniferae and more highly developed families" of the angiosperms. MEYEN (**21**) held essentially the same views as SCHLEIDEN.

TREVIRANUS (**36**) disagreed with SCHLEIDEN and MEYEN, believing that the central portion of the flower of *Viscum album* constitutes an ovary, within the solid tissues of which the embryo sacs arise.

The investigations of HOFMEISTER (**13**) greatly advanced our knowledge of the floral organs of the Loranthaceae, he being the first to study the origin and development of the flowers. His extremely accurate observations were made on *Loranthus europaeus* and *Viscum album*. In these forms the flowers are axillary in origin and position. According to HOFMEISTER, soon after the sepals and carpels have appeared in *Loranthus* the apex of the floral axis elongates, growing up between the carpels and forming a small cone-shaped mass of tissue which later becomes united with them. He found that the embryo sacs are formed in the elongated floral axis which he regarded as "a naked ovule." Below this "ovule" is a little plate of collenchymatous tissue which he believed to be chalazal in nature. He also found that the floral parts in *Viscum album* originate quite similarly to those in *Loranthus europaeus* except that there is no swelling of the floral axis between the carpels, which finally fuse to form a single mass of tissue. The embryo sacs, which are usually two in number, arise from a group of cells in the tip of the floral axis.

VAN TIEGHEM (**37**), from his observations on *Viscum album*, was led to believe that the central mass of tissue of the flower is apical in origin and homogeneous throughout its extent. He described it as being formed by two carpellary leaves, each having its own vascular supply from the peduncle, and becoming "connate" on their "ventral surfaces." He believed that embryo sacs arise

in the lower half of the carpellary tissue, one or two sacs for each carpel. He interpreted the central parenchymatous tissue as a solid ovary, no special segments being differentiated for the production of ovules.

We are indebted chiefly to TREUB (**33**) for an accurate account of the development and a clear interpretation of the reproductive organs of the Loranthaceae. He found in *Loranthus sphaerocarpus* that the tip of the floral axis grows up between the carpels, forming a mammilliform body, the "mamelon," which becomes united to them along their inwardly projecting margins. Between these lines of union with the carpels the "mamelon" is lobed. There are as many lobes as carpels, which are 3–5 in number. An embryo sac is formed in each lobe of the "mamelon." TREUB interpreted these outgrowths of the "mamelon" as rudimentary ovules, and the central region of the "mamelon" he regarded as a placenta. He found in *Loranthus pentandrus* but a slight elevation of the floral axis between the carpels which he called a "rudimentary placenta" and in which the embryo sacs are formed. TREUB (**35**) described a still greater reduction in the floral parts of *Viscum articulatum*, in which there is no projecting placenta or "mamelon." The embryo sacs in this species arise from sub-epidermal cells of the sunken apex of the receptacle. JOST (**15**) described later a similar condition in *Viscum album*.

According to JOHNSON'S (**14**) account of his observations on *Arceuthobium Oxycedri*, there is at the time of pollination a projection of the floral axis which fills the entire ovarian cavity but does not fuse with its walls. He has shown that in opposite sides of this body two embryo sacs are formed, each of which arises from a hypodermal cell. JOHNSON assigns the same morphological value to the elongated axis that TREUB did for *Loranthus sphaerocarpus*. He describes the anthers as sessile on the segments of the perianth and without vascular bundles.

A few years later, PEIRCE (**24**), in his studies on *Arceuthobium occidentale*, confirmed JOHNSON'S account of the morphology of the fruit. His observations together with those of YORK (**43**) on *Phoradendron flavescens* are the most detailed which have been made on the fruit of the American Loranthaceae.

During May and June of 1910, observations were made on 18 different species belonging to 8 different genera of Loranthaceae occurring in Jamaica, and material was collected for a detailed study of their development. From a part of this material the following study was made. This paper, which embodies the results of the beginning of a comparative study of the morphology and physiology of the North American Loranthaceae, embraces an account of the origin and development of the embryo sac and embryo of *Dendrophthora opuntioides* and *D. gracile*, together with a discussion of the physiological relation existing between the gametophyte and sporophyte of these plants. Although this study may lead to the extension of our knowledge of the life histories and relationships of certain genera of the Loranthaceae, and perhaps to a clearer understanding of the systematic position of this family, one of the most interesting as well as most difficult problems for solution will be the determination of the factors which have caused the striking modification and adaptations in the reproductive organs. The material on which this study was made was killed in medium chromacetic acid and cut in sections 10 μ in thickness.

To Professor DUNCAN S. JOHNSON the writer wishes to express his sincere thanks and appreciation for helpful criticism and advice.

Dendrophthora opuntioides

Dendrophthora opuntioides (L.) Eich. receives its name from its *Opuntia*-like appearance (text fig. 1). It is a bright yellowish green, glabrous shrub, seldom more than 4 dm. in height. The stems are jointed, constricted at the nodes, and all the joints of a branch are strongly flattened in one plane. The secondary branches arise in this plane in the axils of the reduced scalelike leaves at the nodes. The internodes are usually paddle-shaped, tapering toward the base. The flowers are opposite, isolaterally arranged in spikes which arise from the nodes of the younger portions of the stem in the same manner as the vegetative branches. The spikes thus formed are strongly flattened structures, whose plane of flattening is parallel with that of the stems. The position of a branch as it develops may vary somewhat from the plane in which the stems are flattened, so that all parts of the whole plant do not always lie

in one plane. However, the whole plant is essentially a single isolateral system.

D. opuntioides as observed in Jamaica occurs in well lighted positions at elevations of 2000–5500 ft. above sea-level. It was found most frequently on the following named plants: *Oreopanax*

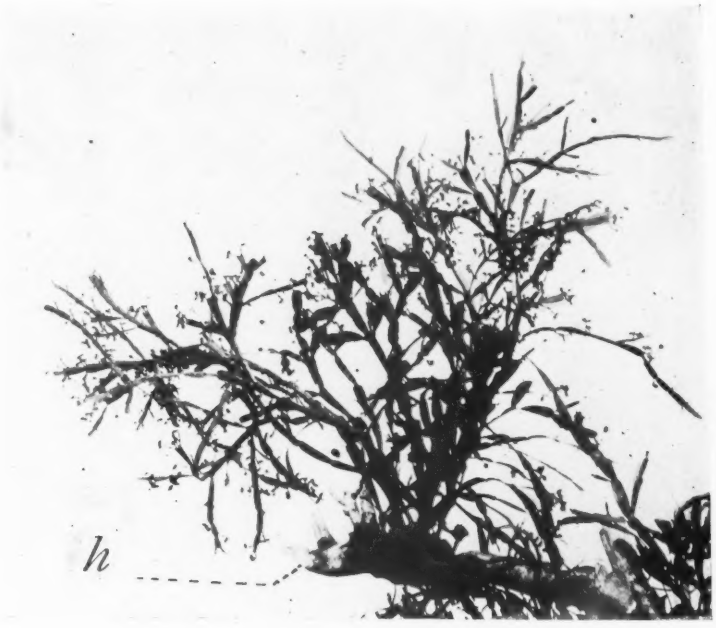

FIG. 1.—*Dendrophthora opuntioides*: *h*, branch of host

capitatum Decne. and Planch., *Rhytidophyllum tomentosum* Mart., *Baccharis scoparia* Sw., *Heterotrichum patens* DC., and *Byrsonima* sp.

Dendrophthora gracile

Dendrophthora gracile Eich. is dark yellowish green in color and is quite similar in appearance and mode of branching to *D. opuntioides*. The branches, however, are often almost terete, and the tendency toward an isolateral arrangement of the branches is less prominent than in *D. opuntioides*. The flowers may be

arranged as in the latter, but they often show a tendency toward a decussate or whorled arrangement. The plants are distinctly dioecious, both forms being exactly alike in external appearance, except that the staminate flowers are usually more densely crowded on the spikes. The anthers are unilocular and sessile on the segments of the perianth. *D. gracile* was found at altitudes of 5000–6500 ft., in well exposed places. It was observed mostly on *Vaccinium meridionale*.

The spikes

Since these two species of *Dendrophthora* are so much alike, the following descriptions, which are drawn primarily from *D. opuntioides*, will be understood to apply to both unless otherwise stated. Each spike is usually composed of two or three internodes, and at the base of each internode there is a pair of connate bracts (figs. 3, 6). Primary growth of this axis is accomplished by the activity of an apical group of initials (fig. 2). There is considerable secondary elongation of the spike, due to an intercalary growth zone at the base of each internode.

A single pair of flowers is usually borne in each internode with the exception of the basal one (fig. 3). They arise laterally just below the apex of the spike, and are at no time closely associated with the bracts at the base of the internode, that is, they do not seem to be axillary in position (figs. 4, 5). In other spikes, which occur less frequently, there are often two or three pairs of flowers on each internode; of these the terminal pair is evidently older, and if three pairs are present, the basal pair is youngest of all (fig. 6). The appearance of these internodes, when the flowers are nearly mature, suggests that the second and third pairs have arisen successively during the intercalary growth of the internode, and that they have arisen from the young tissue at the base of the internode while this portion was still surrounded by the subtending bracts. This phenomenon, which seems unusual in these species, was noted by EICHLER (**7**) in *Dendrophthora Mancinellae* Eichl., and is a characteristic feature, for example, of the inflorescence of *Phoradendron crassifolium* Pohl., where the number of flowers on each internode is much greater than in *D. opuntioides*.

The vascular system of the spike is comparatively simple. From each spike there enter the stem 6–14 vascular bundles, which are arranged as in a typical dicotyledonous stem except that there is no interfascicular cambium (text fig. 7). Growth in thickness is entirely by the divisions of the fascicular cambium and the parenchyma cells between the bundles. A single leaf trace passes from each segment of the perianth into the axis of inflorescence. The paths of the bundles were traced in detail through the basal internode, the first node above the stem, and the first pair of flowers. One bundle, which is entirely free from the others, extends from each of the two connate bracts into the axis. The first pair of bundles on the right and left sides of the axis furnishes the traces for the swollen collar of the stem surrounding the flower. With these same bundles the vessels of the flowers are connected (text figs. 7, 8). The bundles beyond the first pair of flowers were not followed closely, but their distribution is apparently similar to the portion of the system here figured and described.

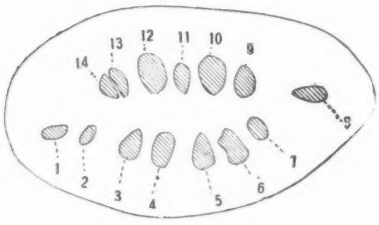

FIG. 7

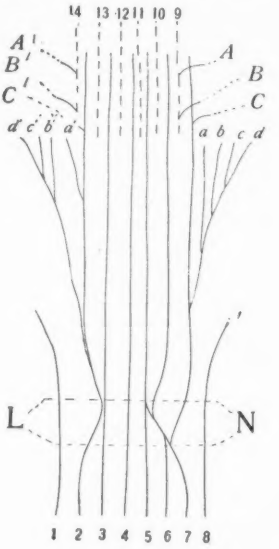

FIG. 8

FIGS. 7, 8.—Fig. 7, cross-section near base of spike, indicating arrangement of vascular bundles; fig. 8, diagram showing arrangement of vascular bundles in lateral view in the first node and first pair of flowers of fig. 3: *1*, *2*, *3*, *4*, *5*, *6*, *7*, *8*, same as in fig. 7; *LN*, level of first node; *1*, *8*, bundles entering the bracts; *a*, *b*, *c*, *d*, *d́*, *b́*, *ć*, *d́*, tracheid strands entering the swollen portion of the inflorescence axis (fig. 4, *c*) about flower; *A*, *B*, *C*, *Á*, *B́*, *Ć*, bundles entering inflorescence axis from the flower (figs. 13, *v*, 20, *v*); *9*, *10*, *11*, *12*, *13*, *14*, as in fig. 7.

The flower

The earliest stage obtained in the development of the flower shows that it is not axillary in origin, but is initiated by a bulging out of the periblem of the inflorescence axis some distance above the axil of the subtending bract (figs. 4, 5). The flowers of *Rhopalocnemis phalloides* have a similar origin, as was shown by LOTSY (**20**). Following such a stage, the surrounding tissues of the incipient floral axis expand rapidly, which results in it becoming almost completely buried within the axis of the young spike (figs. 4, 9). Two cycles of floral segments develop acropetally on the young axis of the flower. The outer consists of three parts, which are the segments of the perianth; while the inner is composed of two segments, the carpels. The perianth completely covers the apex of the floral axis before the carpels have begun to develop (fig. 10). The two carpels arise as distinct primordia, and upon elongating inclose the moundlike apex of the floral axis between them (fig. 11). At this period of development the flower is still sunken in the axis of the spike, and its various parts are clearly distinct from one another (fig. 12, text fig. 12*a*). The apical growth of the floral axis is never active, and the outer region, composed of torus and the basal portion of the carpels, now grows rapidly, and thus the axis with the narrow ovarian cavity about it becomes deeply sunken within the torus (fig. 13). According to GOEBEL (**9**), there is a somewhat similar uprising of the torus and carpels

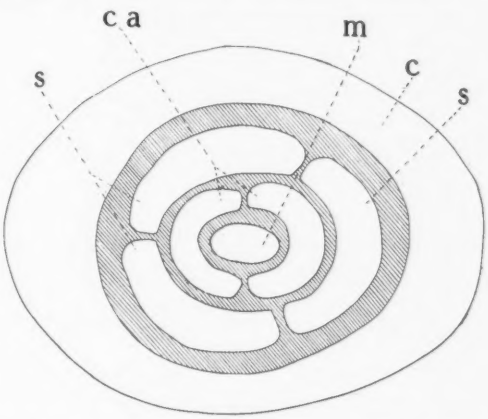

FIG. 12*a*.—Diagrammatic cross-section of flower taken at *AB*, fig. 12: *m*, floral apex or "mamelon"; *ca*, carpels; *s*, sepals; *c*, swollen part of inflorescence axis about flower.

in the early development of the flower of *Pyrus Malus*. The lateral walls of the ovarian cavity are thus lined on the inside by carpellary tissue and the ovary is distinctly epigynous. Meanwhile the moundlike apex of the floral axis has been slowly developing and has come to occupy the entire ovarian cavity. It is in close contact with the walls of the cavity but never becomes united with them. In form, it is a compressed knob, flattened in the same plane with the spike. A transverse mid-section of the knob is oval in outline (fig. 14). A longitudinal section perpendicular to its broad surface is finger-shaped, while a longitudinal section in the plane of flattening shows the knob form (figs. 15, 17, 18).

HOFMEISTER in *Loranthus europaeus* and TREUB in *L. sphaerocarpus* found that the floral axis elongates between the carpels after they have appeared. According to BAILLON (1), the apical part of the floral axis is present throughout the development of the carpellate flower in *Arceuthobium Oxycedri*, just as we have seen it to be in *Dendrophthora*.

The megasporangium (nucellus?)

The floral apex is composed entirely of parenchymatous tissue and has a distinct epidermis. Parallel with the enlargement of the floral axis the cells subjacent to the sporogenous cells divide by periclinal and anticlinal walls (fig. 16). Later, when the uninucleate sac has been formed, it is partially surrounded by a tissue of a few cells in thickness, which has resulted from the divisions of these underlying cells. The contents of the cells of this tissue contain no starch, but have dense cytoplasm, their walls are thicker, and they stain more darkly than the cells of the other portions of the axis (fig. 17). The tissue thus formed about the young gametophyte is apparently nutritive in function, and may be regarded as the equivalent of a nucellus. TREUB has shown that a similar tissue is formed about the archesporial cells in *Loranthus sphaerocarpus*, but the cells are in this case filled with starch. In *Arceuthobium Oxycedri* there is apparently no nucellus formed as in the above mentioned cases. By the time the two-nucleate sacs are developed, the cells of the nucellus have become much enlarged and the axis has become distinctly lobed (figs.

17, 18). A similar though somewhat more marked lobing occurs in *Loranthus sphaerocarpus* (TREUB **33**). The epidermal cells immediately above the sporogenous cells divide by one or two periclinal walls, forming a small cap of cells which is probably to be regarded as the remnant of an integument (fig. 18). WARMING (**38**), in studying the development of the reproductive organs of *Thesium*, found that the contents of the epidermal cells above the apex of the nucellus were more densely granular than the remaining epidermal cells, and that the epidermal cells surrounding these granular ones divide by periclinal walls, forming a tissue about three cells in thickness, which he regarded as vestiges of integuments.

The question of the interpretation of the elongated floral axis, the "mamelon," has been a puzzling one. According to HOFMEISTER, who first worked out its development in *Loranthus europaeus*, it is a "naked ovule" in which there are several groups of archesporial cells present. BAILLON also gave the same interpretation to this body in *Arceuthobium*. TREUB believed that the "mamelon" is a growth of the floral axis in which the separate nucelli represent rudiments of ovules. In reference to HOFMEISTER'S idea, TREUB asserts that there is no reason to consider this hemispherical process as an ovule reduced to its nucellus. Nowhere are groups of embryo sac mother cells formed in the lateral part of a nucellus as would be the case in *Loranthus* if the "mamelon" be regarded as an ovule.

Aucune raison ne nous engage à considérer le processus hémisphérique comme un ovule réduit à son nucelle. Nulle part plusieurs groupes de cellules mères de sacs embryonnaires ne naissent dans les parties latérales d'un nucelle, comme cela serait le cas chez le *Loranthus* si le mammelon en litige méritait le rang d'ovule.

Comparing the enlarged floral apex or "mamelon" as seen in the Loranthaceae with that in certain genera of the Santalaceae, we find a striking resemblance and further evidence for the correctness of TREUB'S views. In the early development of the flower of *Thesium divaricatum*, there is a central elongation of the floral axis as in *Dendrophthora opuntioides* and *D. gracile*. This "mamelon" elongates with the formation of the ovarian cavity and forms a

lobe opposite each of the three carpels. As development continues, these lateral outgrowths enlarge and grow downward along the sides of the axis. These lobes are the ovules. In direction of growth they are anatropous and do not become fused with the placenta along the side of which they grow. Only mere rudiments of integuments are formed, as has been already mentioned. The ovules are thus practically naked. The archesporial cells are subepidermal in origin. In *Santalum album* there is a conelike "mamelon" quite similar to that in *Thesium*, but less extensively lobed. The ovules are without integuments. In *Osyris alba* naked ovules are found on a central placenta as in the two preceding examples, except the ovular lobes at first grow downward and then curve upward toward the apex of the placenta.

From this comparison it is evident that TREUB'S interpretation of the "mamelon" is correct. The two lateral lobes of the elongated floral axis in *Dendrophthora opuntioides* and *D. gracile* are thus rudimentary ovules borne on a central placenta. The micropylar end of the nucellus is toward the base of the placenta, and the chalazal portion lies in the apical part of the floral axis (fig. 17).

The vascular system of the flower

One vascular trace passes from each of the three segments of the perianth into the inflorescence axis. A fourth vessel may enter the axis from near the base of the placenta, but there are no traces in the placenta. The bundles within the segments of the perianth as a rule never branch. About the time of the origin of the one-celled embryo sac, the cells just below the insertion of the placenta begin to enlarge and the walls become unequally thickened. Later there is formed a mass of short tracheids, which are somewhat similar in appearance to water-storage tracheids (fig. 19). This plate of tracheids is analogous to the plate of collenchymatous tissue in *Loranthus europaeus* which HOFMEISTER interpreted as being chalazal in nature. TREUB has shown that a collenchymatous body similar to that described by HOFMEISTER is present in *Loranthus sphaerocarpus*. During the formation of these short tracheids, a series of longer tracheids appear in the outer wall of the ovary at the level of the base of the placenta (text fig. 20, *t*). They

originate thus in or near the zone of elongation of the torus and extend upward from their place of origin, finally fusing with the bundles in the segments of the perianth. Other strands of tracheids pass upward from the plate of tracheids (text fig. 20, *tp*) near the

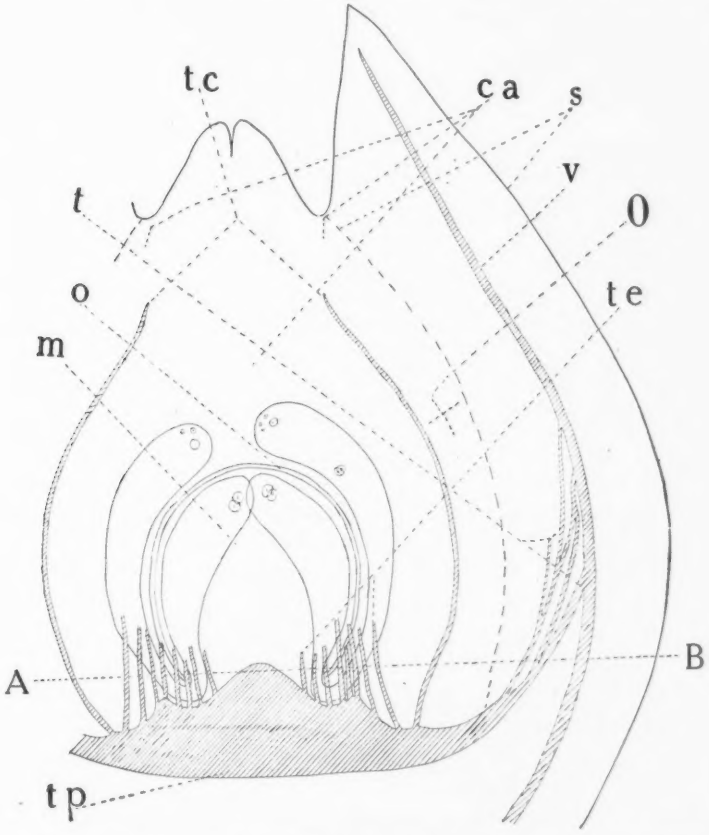

FIG. 20.—Diagrammatic longitudinal section of flower at maturity of embryo sac; *te*, strands of tracheids in inner walls of carpels; *t*, strands of tracheids connecting vascular bundles of the sepals with tracheid tissue beneath "mamelon"; *v*, vascular bundle of sepal; *tp*, plate of water tracheid tissue beneath "mamelon"; *tc*, strands of tracheids in middle region of carpels; *s*, tissue of sepal; *ca*, tissue of carpels; *m*, "mamelon"; *o*, cavity of ovary.

inner walls of the ovary, and by the time of the formation of the mature sac some of them reach almost halfway to the level of the apex of the placenta (text figs. 20, 21, *te*). By the completion of the development of the embryo sac, there are 10–12 vascular traces distributed between the three main bundles of the perianth, with which they have become united (text fig. 21, *t*). Besides uniting with the bundles of the perianth, their branches anastomose with each other, so that in the mature fruit there is an intricate network of vessels within the fleshy pericarp. The vessels, formed in the inner wall of the carpels, constitute their vascular system. The embryo sacs are in close proximity to some of these vessels, while later the endosperm comes to be in direct contact with them. In the ripe fruit the outer coat of the lower half of the seed is formed of remnants of these tracheids.

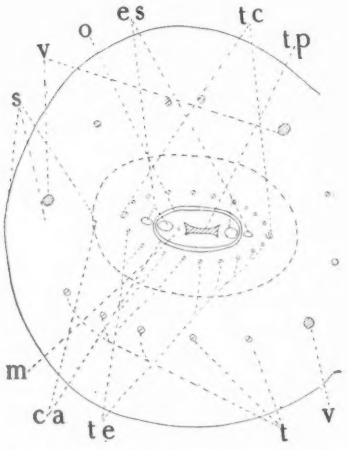

FIG. 21.—Diagrammatic cross-section of flower taken along line *AB* in fig. 20, showing vascular system: *v*, same as *v* in fig. 20 and *A*, *B*, *C*, and *A'*, *B'*, *C'* in fig. 8; *t*, *tp*, *tc*, *s*, *ca*, *m*, *o*, as in fig. 20; *es*, embryo sacs.

Two small strands of tracheids pass upward from the vascular complex in the lower part of the carpels to the base of the style. These strands lie in the plane of flattening of the floral axis (text figs. 20, 21, *tc*). The tissue between these strands is eventually displaced by the endosperm, which then lies in contact with them.

Development of the megaspore

Previous to the upward growth of the torus, as explained above, the archesporial cells become organized. There are two in each "mamelon," hypodermal in origin and located at the poles of the mid-horizontal diameter of the enlarged floral axis (fig. 23). They

are first distinguished by their larger nuclei and more densely staining protoplasm, and without cutting off tapetal cells they develop directly into what may be called megaspore mother cells (fig. 16).

JOHNSON's account of *Arceuthobium Oxycedri* states that the primary archesporial cell divides into two cells. The upper one becomes the primary tapetal cell, which later divides by an anticlinal wall into two cells, while the lower cell becomes "the mother cell of the embryo sac." TREUB'S work shows that no tapetal cells are formed in *Loranthus sphaerocarpus*. He found that the archesporial cell in *Viscum articulatum* does divide into two cells, the lower one developing directly into an embryo sac. It is not possible to determine the character of the upper cell, since it is not known where reduction division occurs.

Preceding division the megaspore mother cell becomes very much enlarged (fig. 16). Later the chromatin thread is organized, becomes thickened, and forms a loose mass, the synaptic knot. Following synapsis, it segments into chromosomes, which later become arranged on the spindle. From two counts of the chromosomes in the dividing megaspore mother cell nuclei of two different ovules at this stage of development, it is apparent that 18–20 chromosomes pass to each pole of the spindle. The same number of chromosomes was found in dividing cells of the young embryo. Thus it seems that no reduction division takes place; hence this division is a normal vegetative division. Since the nucleus passes through what is apparently a synapsis before dividing, it may be regarded as analogous to a megaspore nucleus of the usual type. The two cells resulting from the division of the so-called megaspore mother cell in *Dendrophthora* are separated by a thin wall and lie just beneath the epidermis of the nucellus (fig. 24). The one toward the micropylar region of the nucellus degenerates, while the one in the chalazal portion gives rise to the embryo sac (fig. 25).

In the seed plants in which parthenogenesis is said to occur there is a tendency toward a reduction of the number of divisions of the so-called megaspore mother cell. Four megaspores are formed in *Thalictrum* and *Eualchemilla*. Only two occur in *Taraxacum*

and *Hieracium*, while in *Antennaria* and *Wikstroemia* they have been omitted entirely. The archesporial cell develops directly into an embryo sac in *Balanophora elongata* and *Elastonema acuminatum* investigated by TREUB, and in *Balanophora globosa* studied by LOTSY. The authors claim that the embryo develops apogamously.

In *Arceuthobium Oxycedri*, according to JOHNSON, two small cells are cut off from the lower end of the "embryo sac mother cell." Of the three cells thus formed, the uppermost one, that is, the one toward the micropyle, becomes the one-celled stage of the embryo sac. TREUB has described the same for *Loranthus sphaerocarpus*. He refers to the two lower cells as "anticlines." These authors make no reference to megaspore formation, nor is the place of the reduction division known, yet we may assume that the cells just mentioned are megaspores.

The development of the embryo sac

Two embryo sacs are formed in each ovary, one from each chalazal nucleus, resulting from the division of the megaspore mother cell. Since the development of the two sacs is practically the same, we need follow the history of but one. The cell which gives rise to the gametophyte may be said to become the one-celled sac, and on dividing the two-nucleate sac is formed (figs. 14, 17, 26). No traces of cell walls were observed between these two nuclei. Their division results in the formation of the four-nucleate sac, in which the two nuclei at each pole of the sac are sister nuclei (fig. 27). Simultaneously with the formation of the one-nucleate sac, starch and other food materials are being laid down within its cavity, and by the completion of the four-nucleate stage it is often so densely filled with these substances that the nuclei are almost completely hidden (fig. 28). This is especially true of the sacs of *Dendrophthora gracile*. Ovules of this plant were found in which the nuclei of the sac were either degenerating or had entirely disappeared as a result of the abundant storage of food. In some examples one of the nucelli had been replaced by a cavity filled with food materials (fig. 29). The starch and other organic substances associated with it evidently serve as nourishment for the

further development of the gametophyte, and by the completion of the sac they have usually been entirely consumed. The sac toward the base of the inflorescence as a rule contains a greater amount of stored food substances than its mate, and is the one in which degeneration of the nuclei occurs. No examples were observed where the nuclei in both sacs had begun to disintegrate.

Following this stage, the end of the sac grows almost straight downward in the floral axis until it extends below the level of the insertion of the placenta. It then curves outward into the tissue of the carpel, bends, and grows upward beneath the epidermis of the inner wall of the carpel until the micropylar end of the sac lies almost over the apex of the floral axis (figs. 29, 30). At first it forms a very narrow tube, having a diameter but slightly greater than the width of the cells adjacent to it. It forces its passage through the tissues of the floral axis and the carpel by digesting the cells in front of it. The behavior of the sac suggests strongly that of a pollen tube. GRIFFITH (**11**), in his observations on the Santalaceae, figured and described the branching of the chalazal portion of the embryo sac of *Santalum* and mentioned that it behaved much like a pollen tube. LLOYD (**18**) calls attention to the pollen-tubelike behavior of the embryo sac in his studies of the Rubiaceae. The disintegration of the cells indicates clearly the secretion of an enzyme by the tubelike sac. A portion of the protoplasm in this sac seems to be specialized for this purpose, as will be shown later. As the sac advances, it evidently derives its nutriment from the cells immediately surrounding it. In a sense it is a parasite within a parasite, feeding on the tissue through which it moves. The path of growth of the sac brings it into a most advantageous position for obtaining food. It also provides a line of transit through which food is readily transferred to the developing endosperm and embryo. When the sac grows downward, it comes into direct contact with the vessels at the base of the placenta (text fig. 20). As it turns out into the carpels and grows upward, it is in close proximity to vascular traces from which it draws its nourishment. The cells of the region of the carpel through which the sac moves are richer in protoplasm than the surrounding tissue (fig. 31). No starch was found in these cells, yet their general

appearance and reaction to various stains indicate that they are supplied with some substance which serves as food for the embryo sac. Hence the direction of growth of the embryo sac may be regarded in part as a response to chemotactic stimuli. In *Loranthus sphaerocarpus*, according to TREUB, the embryo sac is surrounded by a sheath consisting of a single layer of cells which are filled with starch. During the development of the long arm from the base of the sac, the portion within the floral axis has been slowly enlarging and advancing upward. The sac as now seen is shaped like a hook, the short arm of which is within the floral axis, while the long club-shaped portion lies wholly within the tissue of the carpel.

The history of the formation of the nuclei of the sac and their arrangement within it are no less interesting to follow than the form of the sac itself. The two nuclei in the chalazal end of the four-nucleate sac become the "antipodals" of the mature sac. They do not divide, but become somewhat enlarged. They are nearly always in close contact with each other, and by the time of the origin of the embryo they may be partially fused. Still later they may become wholly fused (fig. 30), while in other cases they never unite, but remain separate until a very late period in the formation of the endosperm and embryo, when they finally disappear. Coincidently with the downward growth of the sac, the greater portion of the cytoplasm and the two micropylar nuclei, together with most of the food substances, move into the tubelike extension as it is being formed. This mass usually lies a short distance from the apex of the sac as it works its way up through the tissue of the carpel (figs. 32, 33). The cytoplasm which is in contact with the wall of the micropylar end of the sac does not contain starch. It is very dense, finely granular, and stains more darkly than the cytoplasm of the lower portion of the sac, in which the dividing nuclei and food substances are imbedded. With iodine it stains a yellowish dark brown. It is evident that this is a specialized portion of the protoplasm of the sac which probably secretes an enzyme for digesting the tissue as it advances through the carpel. This is evident from the fact that a number of examples were found where the apex of the sac extended up between the cells of the tissue

adjacent to it in the form of pseudopodium-like projections. The cells in contact with these pseudopodia were partially digested (figs. 34, 43). The nuclei of the long arm of the sac are derived from the two micropylar nuclei of the four-nucleate stage, at which period in the development of the sac they are usually a short distance apart. Preceding their division, which begins about the time the sac commences to grow downward, they come together and lie in close contact until after they have divided. They are so intimately associated that in some examples they appear to be partially fused. In the stage preceding the upward growth of the tubelike sac, they are found partially divided in a mass near the tip of the sac, in which 6 nucleoli are distinguishable, some of which are entirely inclosed by a nuclear wall (figs. 35, 36, 38, 39). Examples were found where the sac had advanced well up into the carpel and in which the nuclei had just begun to divide (fig. 34). Either 5 or 6 nuclei are formed, and for some time after the divisions are complete they lie massed together (figs. 32, 37). About the time the tip of the sac has reached to or a little above the level of the apex of the axis, the nuclei of the sac separate, 2 occupying the position of polar nuclei, the other 3 or 4 forming the egg apparatus (figs. 41, 42, 43). The two nuclei corresponding to polar nuclei of a sac of the usual type are sister nuclei, having resulted from the division of one of the two nuclei at the micropylar end of the four-nucleate sac. From the sister nucleus of this same nucleus the nuclei of the egg apparatus are derived. There are 7 or 8 nuclei formed in each sac. If we try to homologize them with the nuclei of a sac of the usual type, we find 2 or 3 cells having the position of synergids accompanying the egg nucleus at the micropylar end of the sac, the 2 just below the egg have the position of polar nuclei, and the 2 in the chalazal region correspond to antipodals. While the long arm of the sac has been developing, the chalazal end has been enlarging and slowly advancing toward the apex of the placenta where it meets the chalazal arm of the sister sac (text fig. 20). At first they are separated by a thin wall, which finally disappears during the early stages of the formation of the embryo, so that the two sacs form one continuous tube (fig. 30).

The embryo sac of *Dendrophthora* as thus seen is quite different

from that known in other Loranthaceae. In *Viscum album*, *V. articulatum*, and *Arceuthobium Oxycedri* the sacs are similar to the common type of embryo sac. In *Loranthus sphaerocarpus* the sac is long and tubular, extending up in the narrow stylar canal. In the two species of *Dendrophthora* which are the subject of this study and *Arceuthobium Oxycedri* the embryo sacs originate in a quite similar manner in the elongated floral axes, which also bear a strong resemblance in general form. The sac in the latter species grows up to the apex of the axis where it is met by the pollen tube. As already shown, there is a strong similarity between the megasporangia of *Dendrophthora*, *Thesium*, and *Santalum*. Also the sacs of *Dendrophthora* and *Santalum* are much alike in their general shape and behavior. In the latter the sac grows downward, curves, and extends upward just outside of the "mamelon." The similarity between the genera of the Santalaceae mentioned above and *Dendrophthora* in the position of the megasporangia and development of gametophytes might be taken as indicative of a phylogenetic relationship.

Of the two sacs formed in each flattened "mamelon," the one toward the apex of the spike becomes functional. The preceding description applies to this sac. It is somewhat larger and usually develops a little more rapidly than its mate. As a rule, the long arm of the latter extends a short distance above the level of the apex of the "mamelon." The development and arrangement of its nuclei are the same as in the micropylar end of the functional sac. Only a few examples of 4 nuclei in the egg apparatus were found.

The divisions of the nuclei of the sac of *Dendrophthora gracile* are usually completed much earlier than those of the sac of *D. opuntioides*. Examples were found in which the nuclei of the long arm of the sac were formed by the time the sac had begun its downward growth (figs. 44, 45). Aside from this difference in time of division the embryo sacs, these two species of *Dendrophthora* are essentially alike. No traces of mitotic divisions of the embryo sac nuclei subsequent to that of the megaspore mother cell were observed until after the maturation of the sac. The chromatic material of the nucleus during this period appears to

have become concentrated into a single nucleolus-like body, which stains uniformly and reacts with Flemming's triple stain, Haidenhain's iron alum hematoxylin, cyanin and erythrosin, thionin, and methyl green and acid fuchsin, as chromosomes do in ordinary mitotic cell division. The division of the nuclei apparently always begins by a fission of this nucleolar mass, which is followed by a constriction of the nucleus (figs. 39, 40). This mass divides into a number of parts equal to the number of nuclei to be formed. For example, in the division of the parent nucleus of the egg apparatus, the nucleolus divides into 3 or 4 parts, each of which later becomes inclosed within a nucleus (figs. 36, 38). The staining reaction and the mode of division of the nucleolus-like body of the nucleus as thus seen clearly indicates that it is composed of chromatin, and instead of dividing into the same number of chromosomes as occur at the time of the division of the megaspore mother cell, it divides only into 3 or 4 parts. Judging from all appearances, the nuclei during the above mentioned period divide amitotically. The manner of the formation of the gametophytic nuclei is apparently quite unique, as the author has found thus far no indication in the literature that such a phenomenon has hitherto been observed in the development of an embryo sac. The mode of division of these sac nuclei is probably stimulated in some way by the presence of abundant food material within the sac.

A number of examples were found where 1–3 small bodies, which stained like the chromatic material in the nuclei of the same embryo sacs in which they occurred or as described in connection with figs. 39, 40, were present in the terminal portion of the embryo sac in the dense finely granular protoplasm mentioned above (figs. 32, 33, *y*). It was not possible to discover their origin or fate.

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EXPLANATION OF PLATES V AND VI

All figures, with the exception of figs. 8, 12*a*, 20, and 21, which are diagrams, are camera lucida drawings from microtome sections. Figs. 3, 6, 22, and 66 were made with a Bausch and Lomb dissecting microscope. In making the remainder of the drawings a Leitz compound microscope was used.

Abbreviations: *a*, floral apex; *an*, antipodals; *b*, bracts; *c*, swollen collar

of the inflorescence axis; *ca*, carpels; *ce*, cutinized epidermis; *cw*, wall of carpels; *d*, definitive nucleus; *dp*, degenerating polar nuclei; *e*, egg nucleus; *ea*, nuclei of egg apparatus; *em*, embryo; *en*, endosperm; *f*, young flower or floral apex; *fn*, fusion nucleus; *i*, rudimentary integuments; *m*, mamelon; *n*, nucellus; *p*, polar nuclei; *pc*, fleshy pericarp; *pl*, placenta; *pi*, pistil; *r*, remains of nuclei of egg apparatus; *s*, stem; *se*, sepal; *sn*, synergid; *st*, starch; *v*, vascular bundle; *vf*, very young flower; *x*, nuclei from which nuclei of egg apparatus and polar nuclei are derived; *y*, chromatin-like bodies.

FIGS. 1, 7, 8, 12*a*, 20, and 21 are text figures.

FIG. 2.—Part of longitudinal section of apex of young spike; ×100.

FIG. 3.—Lateral view of young spike; ×1.5.

FIG. 4.—Part of longitudinal section of apex of spike showing very young flower; ×26.

FIG. 5.—Part of cross-section of young spike showing initiation of flower from periblem; ×100.

FIG. 6.—Lateral view of large spike showing sequence of development of flowers; ×1.5.

FIG. 9.—Outline of cross-section of spike showing sunken flower before sepals have begun to form; ×26.

FIG. 10.—Outline of cross-section of spike showing sunken flowers with sepals; ×26.

FIG. 11.—Longitudinal section of flower showing sepals and incipient carpels (*ca*); ×26.

FIG. 12.—Longitudinal section of terminal portion of inflorescence axis showing young flowers; ×10.

FIG. 13.—Outline of longitudinal section of flower at two-nucleate stage of embryo sac; ×26.

FIG. 14.—Transverse section of "mamelon" at two-nucleate stage of embryo sac; ×100.

FIG. 15.—Outline of longitudinal section perpendicular to broad surface of "mamelon" at two-nucleate stage of embryo sac; ×100.

FIG. 16.—Section of part of "mamelon" showing megaspore mother cell with subjacent cells (*n*) which give rise to nucellar tissue; ×150.

FIG. 17.—Longitudinal section of "mamelon" in plane of flattening, showing two-nucleate sac, nucellar tissue, and placenta; ×150.

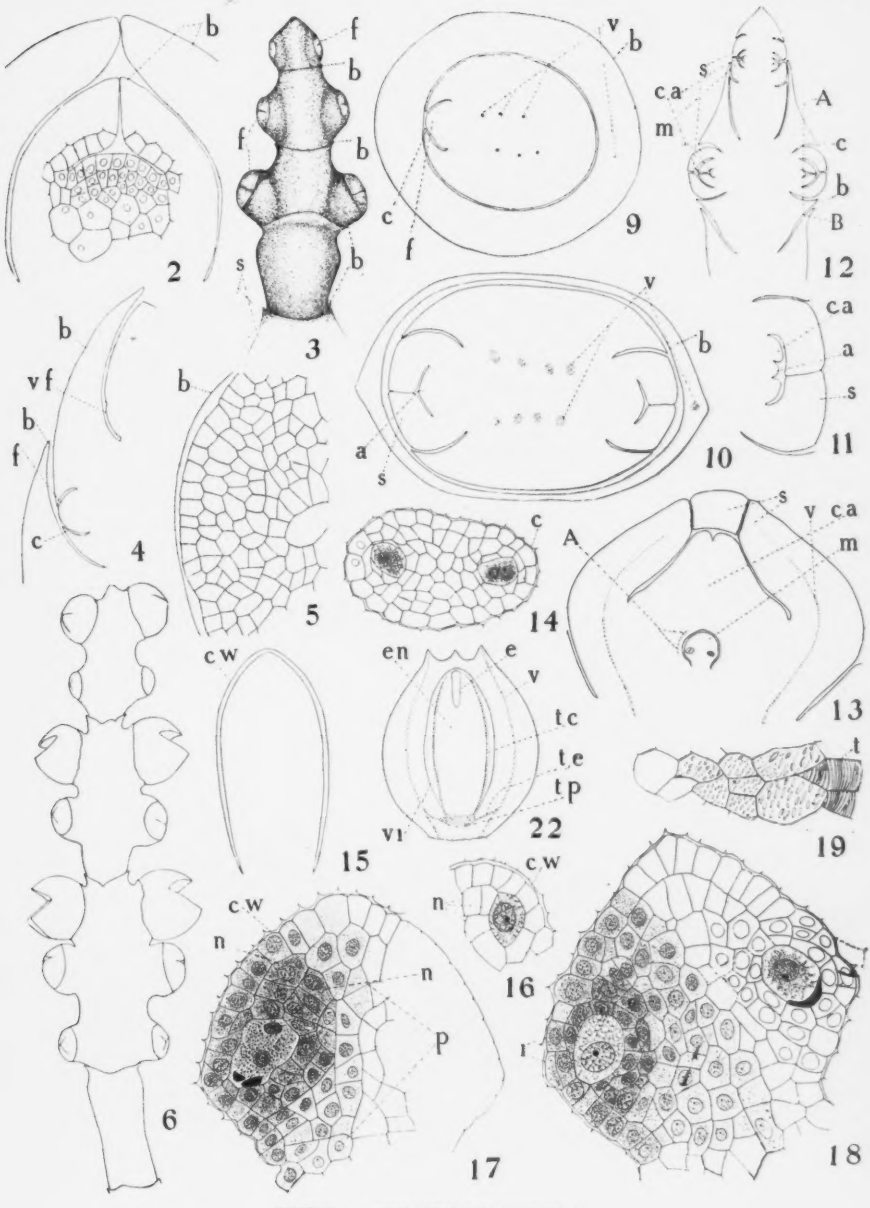
FIG. 18.—Longitudinal section of "mamelon" of *D. gracile* in plane of flattening, showing uninucleate embryo sac and rudimentary integuments (*i*); ×150.

FIG. 19.—Portion of section of tracheid tissue at base of "mamelon"; ×250.

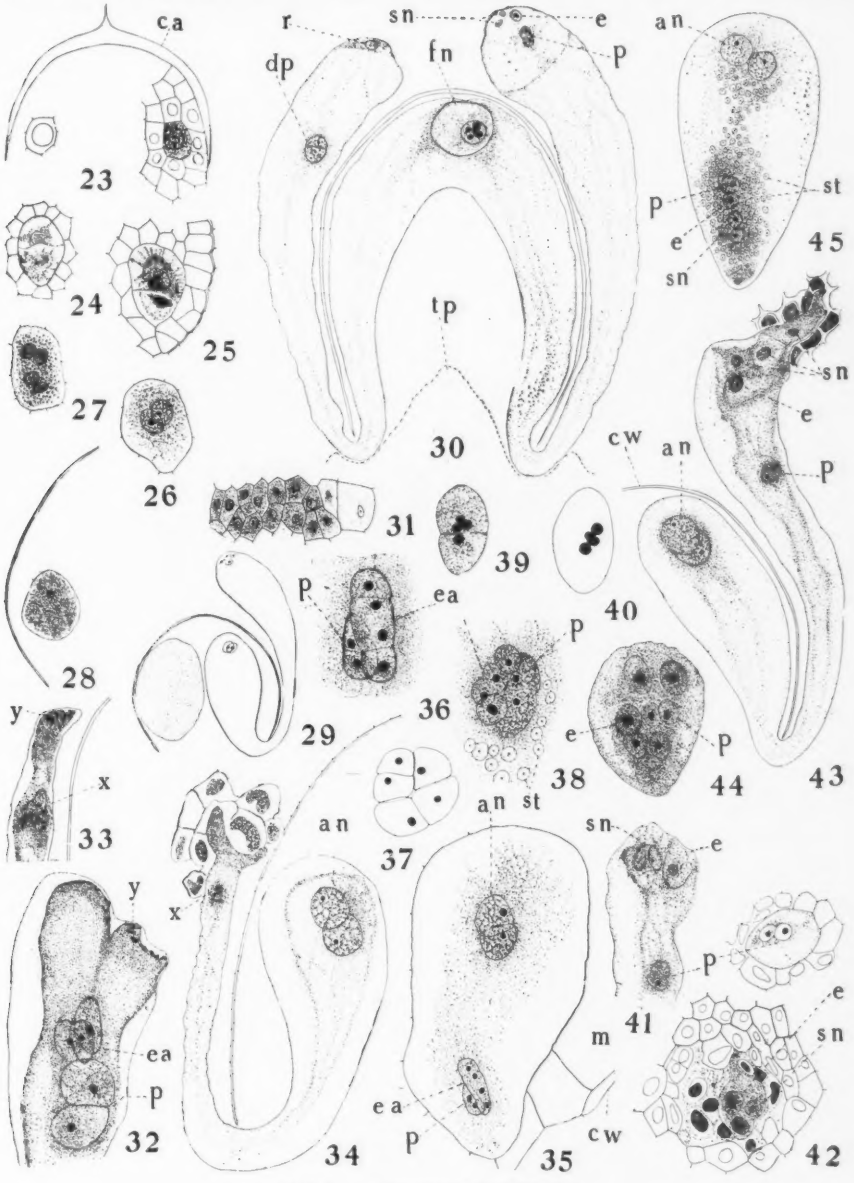
FIG. 22.—Longitudinal section of ripe berry showing embryo, endosperm, pericarp, and vascular system: *tc*, *v*, *t*, *tp*, as in fig. 21; ×1.75.

FIG. 23.—Section of "mamelon" showing archesporial cells; ×100.

FIG. 24.—Part of section of "mamelon," showing megaspores; ×150.



YORK on DENDROPHTHORA



YORK on DENDROPHTHORA

FIG. 25.—Part of section of "mamelon," showing disintegration of basal megaspore; ×150.

FIG. 26.—Longitudinal section of two-nucleate embryo sac; ×150.

FIG. 27.—Longitudinal section of four-nucleate sac; ×150.

FIGS. 28, 29.—Longitudinal sections of "mamelon," showing one of the embryo sac cavities filled with starch; ×100 and 26 respectively.

FIG. 30.—Longitudinal section of flower of *D. gracile*, showing fusion of short arms of embryo sacs, resulting in formation of a single tube; *tp* same as *tp* in fig. 20; ×150.

FIG. 31.—Part of longitudinal section of that portion of the carpel taken at *A* in fig. 13; ×150.

FIG. 32.—Longitudinal section of upper portion of embryo sac, showing polar nuclei, nuclei of egg apparatus, and three chromatin-like bodies (*y*) in terminal portion of sac; ×250.

FIG. 33.—Longitudinal section of upper portion of embryo sac showing chromatin-like bodies (*y*) and group of nuclei from which those of egg apparatus and polar bodies are to be derived; ×250.

FIG. 34.—Longitudinal section of young embryo sac, showing pseudopodium-like projections; ×150.

FIG. 35.—Longitudinal section of young embryo sac which has begun to grow downward, showing dividing nuclei; ×250.

FIG. 36.—Detail drawing of nuclei *ea* and *p* in fig. 35; ×500.

FIG. 37.—Nuclei at micropylar end of sister sac to the sac shown in fig. 35; ×500.

FIG. 38.—Dividing nuclei at micropylar end of sac from which the synergids, egg, and polar nuclei are to be derived; ×500.

FIGS. 39, 40.—Dividing nuclei showing segmentation of the nucleoli; ×500.

FIG. 41.—Longitudinal section of terminal portion of embryo sac; ×500.

FIG. 42.—Cross-sections of mature embryo sac of *D. gracile;* ×150.

FIG. 43.—Longitudinal section of mature embryo sac, showing three synergids, egg, and degenerating polar nuclei; ×150.

FIGS. 44, 45.—Longitudinal section of embryo sacs of *D. gracile* that have just begun to go downward; ×250.

THE PHYSIOLOGY OF THE POLLEN OF TRIFOLIUM PRATENSE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 175

J. N. MARTIN

(WITH ONE FIGURE)

The investigation of red clover pollen was begun with the hope that a thorough knowledge of its physiology, in conjunction with the history of the embryo sac, might help to overcome the uncertainty of clover seed production. The investigation was started at the University of Chicago during the summer term of 1912 and continued at Ames during the autumn of the same year. Many points demand further investigation, but the author thought it well to publish at this time, since the work cannot be resumed until the next growing season. The work has to do with three questions: conditions necessary for the germination of pollen; the stigma as a stimulative and directive factor in tube development; and relative potency of the pollen in self and cross-pollination.

Historical

HANSGIRG (**8**) and LIDFORSS (**9, 11**) succeeded in germinating the pollen of many species in tap water or moist air. The pollen of *Trifolium hybridum* germinated in moist air, but the pollen of *T. pratense* burst. RITTINGHAUS (**5**) found that the pollen of a large number of species would germinate in cane sugar solutions. The optimum concentrations for the different species varied from 20 to 40 per cent. MAX PFUNDT (**14**) showed that 20 to 50 per cent concentrations were required for the pollen of some grasses. KNY (**3**) found that the pollen of *Aesculus Hippocastanum*, *Lilium bulbiferum*, *Robinia Pseudo-Acacia*, *Lathyrus tuberosus*, and *Pisum sativum* germinated better when gelatin was added to the cane sugar solution. MANGIN (**4**) increased the germination in some species by adding either agar or gelatin to the sugar medium. JOST (**12**) found the germination of the pollen of some species of grasses to depend entirely upon the water supply. This he

controlled by germinating the pollen on parchment paper soaked in distilled water and properly dried on filter paper. The pollen of some composites would germinate on the parchment paper only after it had been soaked in sugar solution and then suitably dried. ELFVING (**2**) was unable to germinate the pollen of *Ornithogalum Ecklonii* and some species of grasses except on the stigma. Glycerin, potassium chlorate, and sodium carbonate added to sugar solutions had no effect. HANS MOLISCH (**7**) found that 0.01–0.05 per cent calcium malate or 0.01 per cent malic acid added to the sugar solution would cause the pollen of *Azalea* and *Rhododendron* to germinate. Saltpeter, asparagin, citric acid, and tartaric acid had a slight stimulative effect. LIDFORSS (**9**) increased the percentage of germination in some species of *Erica* and *Menziesia* by the addition of a small percentage of citric acid. VAN TIEGHEM (**1**) obtained better germination in some species by adding ammonium bitartrate to the medium. SANDSTEN (**16**) found that tomato pollen required a slightly acid medium. BURCK (**12**) observed that the pollen of certain species of *Mussaenda* would germinate in distilled water, but only when a portion of the stigma or levulose was added. Levulose could not be replaced by other sugars. TISCHLER (**15**) was able to germinate the sterile pollen common in *Solanum rostratum*, in some of the Commelinaceae, Melastomaceae, Pontederiaceae, Liliaceae, Lythraceae, and in the genus *Cassia* of the Leguminosae, by adding diastase to the sugar solution. According to LIDFORSS (**9**), the presence of a small percentage of calcium or potassium salts or a lack of aeration will prevent germination in many species. BURCK (**12**) found that levulose inhibited germination in *Pavetta* and *Antirrhinum* and caused bursting in *Murraya exotica*. The work of MOLISCH (**6, 7**) showed that the direction of pollen tubes in some species is due to carbohydrates, and in other species to negative aerotropism. LIDFORSS (**10**) found that proteins attract the pollen tubes in some species. In the species investigated by KNY (**3**) gravity and light had no directive influence on the pollen tubes. Some of the earlier botanists, and more recently LINDHARD (**17**), and the work carried on by PAMMEL and COE, which is not yet published, have shown that the pollen of *Trifolium pratense* is impotent on its own stigma.

Description of the pollen

The pollen grains mature very early in the history of the flower, the stamens and pistil being about 0.25 mm. in length and the integuments barely appearing on the ovules when the mother cells divide. When the embryo sac is mature the pollen grains are binucleate. They are almost globular when turgid, with a little flattening around the germ pores, and have an average size of 44.5 $\times 43\,\mu$. The pollen is plasmolyzed when shed from the anther, and one diameter is much shortened by an infolding of the wall. The average dimensions in this condition are $26 \times 48\,\mu$.

CONTENT.—Pollen treated with chloral hydrate and iodized potassium iodide gave no starch reaction. The immediate bursting of the pollen in these solutions permits good exposure of the contents and makes observations easy. Treated with Sudan III, the numerous small particles giving the pollen content its granular appearance gave a definite fat reaction. This fat exists in the form of a fine emulsion.

OSMOTIC PRESSURE.—In determining the osmotic pressure, sucrose solutions were used, since the pollen seems less permeable to this sugar. Volume-normal (mol. wt. dissolved to a liter volume of solution) solutions were used in watch glasses, which were sealed to prevent evaporation and left on the laboratory table. The results are given in table I.

TABLE I

Time	1.5 volume-normal	2 volume-normal	2.33 volume-normal	2.5 volume-normal	2.66 volume-normal
10 m....	Turgid	Turgid	Plasmolyzed	Plasmolyzed	Plasmolyzed
20 m....	"	"	"	"	"
30 m....	"	"	"	"	"
1 hr....	"	"	"	"	"
7 hrs...	"	"	5 per cent turgid	"	"
20 hrs...	"	"	10 per cent "	"	"
48 hrs...	"	"	20 per cent "		

The table shows that a 2.33 volume-normal solution is a little weak, provided the pollen grains are not permeable to the solution; but 2.33 volume-normal is nearer the proper strength than 2.5. If 2.33 volume-normal is changed to weight-normal (mol. wt.

dissolved in a liter of water) and calculated for 25° C. according to data and formulae given by RENNER (**18**), it gives an osmotic pressure of 163.5 atmospheres. This takes no account of the excessive increase of pressure over concentration between 4.13 and 4.65 weight-normal (2.33 volume-normal). The pollen was permeable to saturated solutions of KNO_3 and NaCl, and these salts could not be used for determining osmotic pressure.

Germination of pollen

The pollen of *Trifolium pratense* bursts almost instantly when dropped into water, so any suitable medium must control water absorption. Small amounts of sugar solutions made up in double distilled water by the volume-normal method were used in the ordinary watch glasses, carefully cleansed. The flowers were collected between 9 A.M. and 3 P.M. and the pollen from those well open, but still fresh, was used. The dishes, sealed with glass plates and vaseline, were left on the laboratory table and observations were made about every 30 minutes during the three or four-hour test period. Table II shows the effects of different sugar solutions on the pollen of *Trifolium pratense*, *T. hybridum*, and *T. repens*.

Decoctions of the stigmas alone or in distilled water, as well as those made by grinding the stigmas in the sucrose and levulose solutions given in table II, gave no germination in *Trifolium pratense;* 0.000075, 0.000375, and 0.075 volume-normal solutions of malic acid, as well as equal concentrations of calcium malate, added to the sugar solutions gave increased bursting in *T. pratense* and reduced the percentage of germination in *T. hybridum* and *T. repens*. A 0.000277 volume-normal of HCl or a 0.00056 volume-normal of butyric acid used with the sugar solutions had little effect. The butyric acid gave a little better germination in *T. hybridum* and *T. repens* in sucrose solutions above 0.731 volume-normal. Stronger solutions of either acid increased bursting and cut down germination. Sugar solutions containing agar or gelatin allowed less bursting, and 2 grams to 5 grams of gelatin added to a 0.731 volume-normal solution of sucrose gave the best medium for the pollen of *T. hybridum* and *T. repens*. Pollen of *T. pratense* run in sugar solutions under increased pressure of oxygen and

TABLE II

SHOWING THE EFFECTS OF DIFFERENT SUGAR SOLUTIONS ON THE POLLEN OF *Trifolium pratense*, *T. hybridum*, AND *T. repens*

Solution	Volume-normal	*T. pratense*	*T. hybridum*	*T. repens*
Double distilled H_2O		Immediate bursting	Immediate bursting	Immediate bursting
Sucrose	0.1462	Bursting	Bursting	Bursting
"	0.2824	"	"	"
"	0.4386	"	Bursting 25; germination	Bursting 25; germination
"	0.5848	About 50 burst; no germination	About 80 per cent germination	About 80 per cent germination
"	0.731	Turgid	Good germination	Good germination
"	0.8772	"	" "	" "
"	1.0233	"	" "	" "
"	1.1695	"	Plasmolysis	Plasmolysis
"	1.3217	"	"	"
"	1.4619	"	"	"
Levulose	0.833	Bursting	Some germination and much bursting	Some germination and much bursting
"	1.1108	About 50 per cent bursting	Fair germination; no bursting	Fair germination; no bursting
"	1.3888	Turgid; no bursting	About 50 per cent germination; no bursting	About 50 per cent germination; no bursting
"	1.666 2.2216 2.499 2.7776	Turgid; no bursting	About 50 per cent germination; no bursting	About 50 per cent germination; no bursting
Dextrose	1.1108	Bursting	Bursting	Bursting
"	1.3888	"	Feeble germination; some bursting	Feeble germination; some bursting
"	1.666	"	Feeble germination; some bursting	Feeble germination; some bursting
"	1.9333	"	No bursting; 25 per cent germination	No bursting; 25 per cent germination
"	2.2216 2.499 2.7776	"	No bursting; 25 per cent germination	No bursting; 25 per cent germination
Maltose	0.5848	"	Bursting	Bursting
"	0.731	Some bursting	Feeble germination; some bursting	Feeble germination; some bursting
"	0.8772	Bursting	Feeble germination; some bursting	Feeble germination; some bursting
"	1.0233	"	No bursting; 25 per cent germination	No bursting; 25 per cent germination

TABLE II—*Continued*

Solution	Volume-normal	*T. pratense*	*T. hybridum*	*T. repens*
Maltose...	1.1695 1.3217 1.4619	Bursting	No bursting; 25 per cent germination	No bursting; 25 per cent germination
Percentages of maltose and dextrose mixed gave about the same results				
Lactose...	0.5848	Bursting	Bursting	Bursting
" ...	0.731	"	50 per cent germination; some bursting	50 per cent germination; some bursting
" ...	0.8772	"	50 per cent germination; some bursting	50 per cent germination; some bursting
" ...	1.0233 1.1695 1.3217 1.4619	"	50 per cent germination; no bursting	50 per cent germination; no bursting
Arabinose	1.3333	"	Bursting	Bursting
"	1.6555	"	50 per cent germination; some bursting	50 per cent germination; some bursting
"	1.9999	"	50 per cent germination; no bursting	50 per cent germination; no bursting

carbon dioxide showed that the supply of these gases was not the limiting factor. Small dishes made by cutting off glass shells about one-half inch from the bottom and containing the pollen in very shallow depths of sucrose and levulose solutions, which did not permit bursting, were placed in wide-mouthed bottles and attached to oxygen and carbon dioxide tanks. No germination resulted from a three-hour exposure to an increased pressure of these gases. In table III the results obtained with other media are given.

Results obtained by use of parchment paper and animal membrane with pollen of Trifolium pratense and T. hybridum

Small squares of parchment paper were soaked in distilled water and in 0.5848, 0.731, and 0.8772 volume-normal sucrose solutions and then dried on filter paper until surplus moisture was removed, mounted on slides, and after application of pollen placed

under bell jars on the laboratory table. Parchment paper proved unsatisfactory because its opaqueness and fibrous character made observation difficult; so after several sets were run with no germination, hog bladder was substituted. After a few trials good

TABLE III

SHOWING THE EFFECTS OF VARIOUS SOLUTIONS ON THE POLLEN OF *Trifolium pratense*

Solutions				
Sucrose 0.731+KNO_3 0.00006	Bursting			
Sucrose 0.731+KNO_3 0.0002	About 25 per cent bursting	75 per cent turgid	No germination	
Sucrose 0.731+KNO_3 0.0006	About 25 per cent bursting	75 per cent turgid	"	"
Sucrose 0.731+KNO_3 0.002	Very little bursting	Turgid	"	"
Sucrose 0.731+KNO_3 0.005	No bursting	"	"	"
Sucrose 0.731+galactose 1.3888 + a trace of asparagin	Very little bursting	"	"	"
Sucrose 0.731+asparagin 0.0375	Bursting			
Sucrose 0.731+dextrose 1.3888 +KNO_3 0.0005	Little bursting	25 per cent or more turgid	"	"
Sucrose 0.731+0.0075 asparagin	About 50 per cent bursting	50 per cent turgid	"	"
Sucrose 0.8772+dextrose 1.666 +asparagin 0.075	Bursting	.....	.....	
Sucrose 1.0233+asparagin 0.15	"	.....	.....	
Sucrose 0.8772+galactose 1.9333+asparagin 0.187	"	.....	.....	
Sucrose 0.8772+asparagin 0.0015	No bursting	Turgid	"	"
Sucrose 0.8772+asparagin 0.00075	" "	"	"	"
Sucrose 0.8772+asparagin 0.000375	" "	"	"	"
Sucrose 0.8772+glycerin oleic acid	" "	"	"	"
Sucrose 0.8772+palmitic acid	" "	"	"	"
Sucrose 0.8772+lipase	" "	"	"	"
Levulose 1.666+lipase	" "	"	"	"
Lecithin+H_2O as a thick paste	" "	"	"	"
Sucrose+lecithin as a thick paste	" "	"	"	"
Levulose+lecithin as a thick paste	" "	"	"	"
Sucrose 0.8772+diastase	" "	"	"	"

germination was obtained on the bladder. It was found that germination was very closely connected with the amount of water in the membrane, and it was not easy to dry the membrane so as always to secure germination. Membranes soaked in

0.731 and 0.8772 volume-normal solutions of sucrose or in 1.3888 and 1.666 volume-normal solutions of levulose and properly dried gave as good results as those soaked in distilled water. This shows that these sugars have no toxic effect on the pollen. The efficiency of the membrane did not depend upon the fats or salts contained, for pieces extracted 5 days in alcohol and ether in a Soxhlet's extraction apparatus or boiled for 16 hours in changes of distilled water did not lose their efficiency, although their physical properties were so changed that the requisite amount of soaking and drying had to be found again by experimentation. Another series of trials with parchment paper showed it to be as effective as the bladder and that the previous failure was due to insufficient drying. In these tests most attention was given to the pollen of *T. pratense*, although the pollen of *T. hybridum* was investigated sufficiently to discover that it germinated readily on the membrane and that its germination would permit more variation in the water content of the membrane than the pollen of *T. pratense*.

The nature of the germination of the pollen of *T. pratense* on the membrane needs some discussion. Germination was not uniform. On some portions of the membrane the percentage of germination was high, while on other portions there was no germination. These different regions were usually quite definitely marked off, and the germination in a region was usually good or none at all. This lack of uniformity was mainly due to a difference of texture, composition, or thickness of these regions. A difference in these properties would make a difference in the amount of water supplied to the pollen in the different regions. Some variation no doubt exists between pollen from different anthers and between pollen grains from the same anther in respect to the water supply requisite for germination. But in mounting the pollen, the keel was sprung with a scalpel, and as the pollen was thrown from the anthers, it was collected on the instrument and then spread on the membrane. By this method of collecting and mounting, the pollen was well mixed, and the variation of the pollen would not account for all of the lack of uniformity in germination.

The percentage of germination determined by taking into account all the pollen on a membrane when any germination occurred

varied from almost zero to 96 on different membranes. Still, on membranes with the low percentage of germination, the percentage of germination was high in the region where it occurred. In table IV are given the results obtained on a small piece of bladder that gave fairly uniform germination.

TABLE IV

Total number of pollen grains	Number of germinations	Percentage of germination
107	87	81+
135	110	81+
209	183	87+
176	170	96+
126	101	80+
153	144	94+

The time required for germination at room temperature was 8–10 minutes. This agrees with SANDSTEN'S (**16**) report on *T. hybridum* and *T. repens*.

The lengths of tubes produced were various. The maximum length of tubes measured was about 15 times the diameter of the pollen grain. The lengths of the majority ranged from 6 to 15 times the diameter of the pollen. It is probable that much longer tubes would have been produced if the water delivery of the membrane had remained constant.

The results obtained with the membrane and parchment paper showed that the water supply was at least the important factor if not the only factor in determining germination.

An attempt was made to secure the proper water supply by means of sugar solutions. Sucrose solutions with a difference of 0.0877 volume-normal and ranging from 0.731 to 2.2 volume-normal were used. The only germination obtained in these solutions was less than 0.5 per cent in 1.7 volume-normal. In accounting for this failure, three things should be considered: (1) the range of water supply permitting germination may be so small that it was missed by these concentrations; (2) the supply of oxygen and carbon dioxide might have been limiting factors since the higher concentrations were greater than those run under the increased pressure of these gases; (3) the condition for germina-

tion may be a certain ratio between the amount of water taken up and transpiration.

An effort was made to reduce this required water supply to some definite expression by running tests on bladder suspended over different concentrations of H_2SO_4. Gram-molecular solutions were placed in large, wide-mouthed bottles fitted with rubber corks. A glass tube about 10 inches in length was run through the rubber cork and the membrane suspended from a cork fitted over the lower end of the glass tube. With the upper end of the tube corked, the apparatus was left in the required temperature 48 hours to secure moisture equilibrium between liquid and membrane. If stored longer than 48 hours fungi gave trouble. The pollen was collected on the end of a glass rod and deposited on the membrane by running the rod through the glass tube. This method prevented interchange between outside and inclosed air. The percentages of moisture were approximated from data given in LANDOLT-BÖRNSTEIN (**19**). The humidity at the pressure of saturation over pure water was considered 100 per cent, and moisture for each temperature used and the percentages over the solutions are based on the 100 per cent. The results of two series run are given in full to show variation and the others are summarized (tables V–VII).

TABLE V

TEMPERATURE 35° C.

Gram molecular of H_2SO_4	Relative percent. of moisture	No. of pollen grains	Percent. of germinations	Condition
1	95.5	1201	0.88	Turgid
0.7	96.5	2187	17.4	Some bursting
0.5	97.2	1801	29.9	Little bursting
0.3	98.6	2209	10.0	20 per cent bursting
Pure H_2O	Some less than 100	2736	24.4	30 per cent bursting

TEMPERATURE 20° C.

1	95.5	1120	0	Turgid
0.7	96.5	1396	0.21	"
0.5	97.2	1590	0.12	"
0.3	98.6	1340	1.34	Little bursting

TABLE VI

RELATIVE PERCENTAGE OF MOISTURE 98; GRAM-MOL. 0.5 H_2SO_4; TEMPERATURE 35° C.

No. of sets run	No. of pollen grains	No. of germinations	Percentage of germinations	Condition
1st	208	0	0	Turgid
2d	200	0	0	"
3d	198	0	0	"
4th	205	125	60.9	"
5th	223	146	64.5	Some bursting
6th	181	5	2.7	Turgid
7th	208	0	0	"
8th	195	165	84.6	"
9th	183	98	53.5	"
Totals	1801	539	29.9	

TABLE VII

RELATIVE PERCENT. OF MOISTURE 99; GRAM-MOL. 0.3 H_2SO_4; TEMPERATURE 35° C.

No. of sets run	No. of pollen grains	No. of germinations	Percentage of germinations	Condition
1st	219	0	0	Turgid
2d	167	0	0	50 per cent bursting
3d	127	0	0	Turgid
4th	132	0	0	"
5th	253	50	19.7	"
6th	218	100	45.8	"
7th	310	10	32.2	Much bursting
8th	435	35	8+	" "
9th	348	26	7.5	" "
Totals	2209	221	10	

As seen from the tables, the percentages of germination in most of the sets run were low as compared with those obtained under bell jar on the laboratory table. This low percentage may be due to three things: (1) the membrane was not in equilibrium; (2) the amount of moisture required by different pollen grains for germination may vary so much that only a small percentage of germination can take place under a given moisture condition; (3) germination may be to some extent connected with transpiration. The marked variation in behavior between sets run over the same solution at the same temperature strongly suggests that moisture equilibrium had not been established within the apparatus. The

tables show that for these temperatures germination takes place only when the percentage of moisture is close to saturation.

The influence of the stigma upon the germination of the pollen and upon the direction of the pollen tubes

The stigma presents a very uneven surface due to the projection of the papillae. The exposed portion of the papillae has a rather heavy cutinized wall. Microchemical tests showed no sugar or starches present in the papillae, but an oily emulsion such as was found in the pollen.

Although decoctions of the stigmas had been tried without any positive results, it was thought worth while to try them in connection with the bladder. After the pollen had been spread on the prepared sections of bladder, stigmas from other plants were pressed down on these membranes with a scalpel, and then the sets were run under the bell jar on the laboratory table. These stigmas apparently exerted no influence on germination or on the direction of the pollen tubes. Often there was no germination around the stigma when there was good germination in other regions; and when there was germination around the stigma, germination just as good could be found in other places. The pollen tubes around the stigmas were grown in all directions, and pollen grains in contact with the stigma were found growing tubes at right angles to, and away from, the stigma. From these observations it appears that the stigma secretes nothing that has any effect on germination or the direction of the pollen tube. The behavior of the stigma in the experiments at least indicates that its function in the germination of the pollen is to regulate the water supply; and the nature of the pollen necessitates no other function. If this is the function of the stigma, and the water supply must be as delicately adjusted on the stigma as on the membrane to secure germination, then conditions which will modify the amount of water delivered by the stigma will have an effect on fertilization and hence on seed production. This may account for the usually poor seed production in the early part of the season, since there is usually more moisture in the ground at this time and more rain during the flowering period than occurs during the second crop. If germination depends

upon a certain balance between the amount of water taken up and transpiration, then a variation in the moisture of the atmosphere would have an effect on fertilization.

The comparative potency of pollen in self and cross-pollination

Pollen tubes can be traced through the stylar canal by mounting the pistils in a 30 per cent sucrose solution and flattening with a little pressure on the cover glass. The tubes have a denser and more granular content than the cells of the style and these features make it possible to trace them. Sufficient pressure causes the ovary to break just above the ovules and enables one to see the tubes in the ovary. Fig. 1 shows the upper portion of an ovary with exposed pollen tubes 55 hours after pollination. For self and cross-pollination vigorous field plants were selected, and flowers to be used were put under cover 2 or 3 days previous to opening and remained covered until collected for examination. Flowers were self-pollinated by simply springing the keel. In cross-pollination the keel was sprung, and the pollen collected from another plant was applied to the stigma with a scalpel. An examination of 30 flowers crossed showed the pollen tubes in the ovary 50 hours after pollination. Sections of ovaries killed 55 hours after crossing showed that the egg had enlarged for its first division

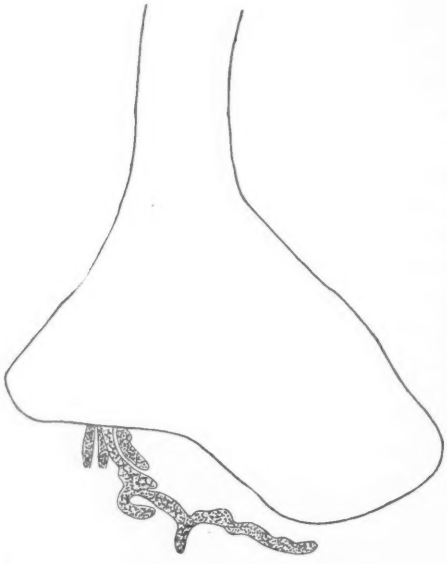


FIG. 1.—Camera drawing, showing the upper portion of an ovary teased off and the pollen tubes invading the ovary.

and that the endosperm cell had made one division; therefore, fertilization must take place about 50 hours after cross-pollination.

An examination of those flowers self-pollinated at the same time the others were crossed showed good germination on the stigma. The number of pollen grains germinating on their own stigma ranged from 3 to 25 in the 30 flowers. The tubes produced were all short, none exceeding 4 mm. Out of 20 self-pollinated flowers run 90 hours, one tube was found with a length of 7.25 mm.; the other tubes varied in length from a fraction of a millimeter up to 5 mm. Counting the average length of the style and stigma 11.5 mm., one is able to compare the rates of growth of pollen tubes in the two cases. The tubes in case of self-pollination look as vigorous as those in cross-pollination. Some abnormal behavior was observed. In one case the tubes were found wound about each other in the upper part of the stylar canal. In a few cases one of the longer tubes had turned back upon itself.

The question is now raised in case of self-pollination as to whether or not the tube can reach the ovary and effect fertilization. Field work on self-pollination shows that it rarely does, if ever.

Summary

The pollen of *Trifolium pratense* is physiologically different from that of *T. hybridum* and *T. repens* in respect to behavior toward sugar solutions.

The only function of the sugar solution in the case of the pollen of *T. hybridum* is the controlling of water supply.

The germination of the pollen of *T. pratense* is delicately adjusted to water absorption.

The results of the investigation show that the stigma produces no secretions which influence pollen tubes.

The nature of the pollen demands no other function of the stigma in its germination than the control of the water supply.

The pollen in self-pollination germinates readily on the stigma, but the tubes traverse the style much more slowly than in cross-pollination.

In conclusion I wish to express my thanks to Dr. WILLIAM CROCKER and Dr. SOPHIA ECKERSON of the University of Chicago,

under whom a greater part of the work was done, for their valuable suggestions; and to Dr. PAMMEL, who gave me valuable assistance at Iowa State College.

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OBSERVATIONS ON THE MORPHOLOGY OF THE AROIDS

JAMES ELLIS GOW

(WITH FORTY-SEVEN FIGURES)

The material for the following observations was collected in the greenhouses of the New York Botanical Gardens, Bronx Park, New York, and was worked up by the writer during the years 1911 and 1912. The usual methods were used, the sections being cut in paraffin, and stained usually by the iron-alum-hematoxylin process, or triple stained with Delafield's hematoxylin, safranin, and orange G. The species are given in the order studied:

1. Aglaonema commutatum

At the time this work was begun, the writer was not aware of the work done by CAMPBELL on this species.[1] The results confirm CAMPBELL's conclusions as to the seven antipodals (fig. 1) and the spherical proembryo (fig. 2). In the specimen here figured, two of the antipodals appear in process of disintegration.

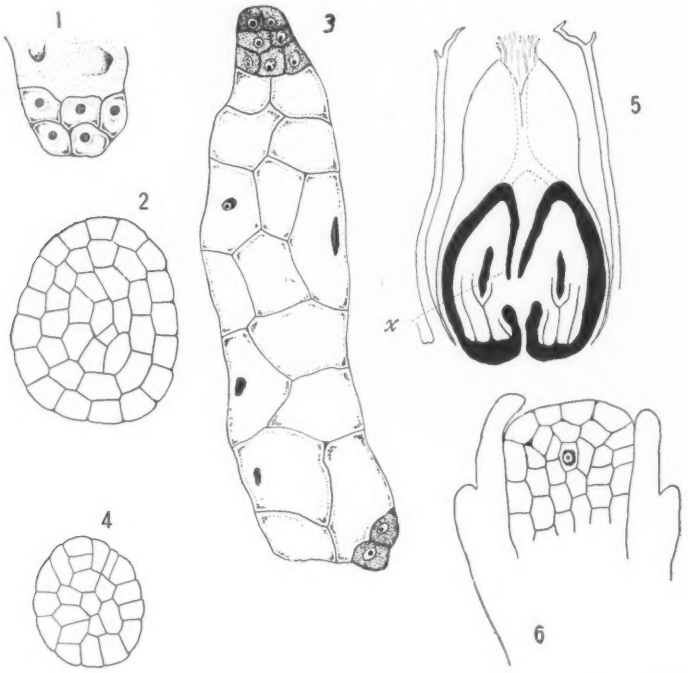
2. Aglaonema nitidum

The staminate flower consists of a synandrium, cleft into lobes by 2–5 shallow creases, each lobe containing a single loculus. The youngest material examined showed the tapetum largely broken down, the pollen grains fully formed, and the first nuclear division completed. The division of the generative nucleus had not taken place. It probably occurs in the tube, and not in the pollen grain.

The pistillate flower consists of a single carpel which contains one basally attached anatropous ovule. The inner integuments are massive, the outer being thinner and never closing over the inner. In the mature embryo sac there are 10 cells, 5 of which occupy the position of antipodals, the other 5 performing the usual functions. The divisions of the endosperm nucleus give rise to a quantity of heavy-walled endosperm (fig. 3). The antipodals, or

[1] CAMPBELL, D. H., Studies on the Araceae. Ann. Botany **14**:1–25. *pls. 1–3.* 1900.

some of them, frequently persist until the sac is quite filled with endosperm. The embryo develops simultaneously with the endosperm, and is at first of the spherical form which appears to be characteristic of this family (fig. 4).



FIGS. 1, 2.—*Aglaonema commutatum:* fig. 1, seven antipodals, two disintegrating; fig. 2, spherical proembryo.

FIGS. 3, 4.—*Aglaonema nitidum:* fig. 3, endosperm; fig. 4, proembryo.

FIGS. 5, 6.—*Anthurium crystallinum:* fig. 5, longitudinal section of ovary, showing two of the six ovules; fig. 6, primary archesporial cell.

3. Anthurium crystallinum

The flowers are perfect, the number of stamens varying from 4 to 6. There is a broad connective, and complete differentiation of filament and anther, in which respect the plant differs from such forms as *Arisaema* and *Aglaonema*. The appearance of the tetrads

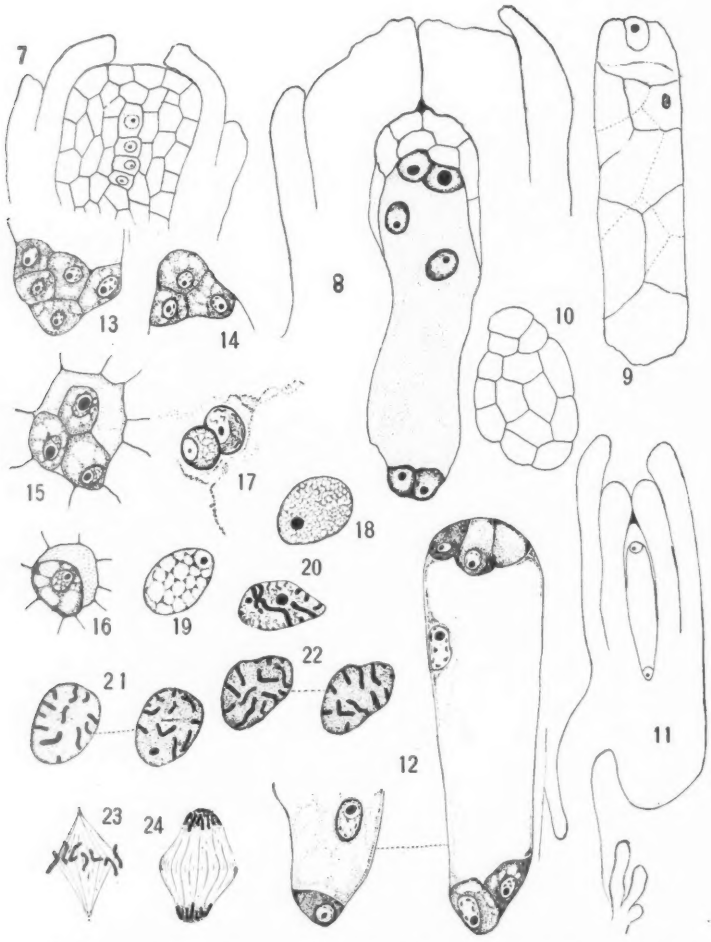
indicates that the divisions are simultaneous. The separation of the two male nuclei follows immediately on the liberation of the pollen grain in the loculus.

The compound ovary consists sometimes of two but usually of three closely united carpels, with a single truncate style whose canal is filled with viscid conducting tissue. Each of the three carpellary cavities contains two laterally attached anatropous ovules (fig. 5). The immature ovules are at first erect, but soon become reversed through the non-development of their lower surfaces. Simultaneously with their reversal, the primary archesporial cell becomes differentiated, and can readily be detected by its heavy chromatin network and ready reaction to hematoxylin stain (fig. 6). Two divisions occur, giving rise directly to 4 megaspores (fig. 7), the lower 3 of which are suppressed and break down. The functioning megaspore increases rapidly in size. The nuclear divisions are of the usual type, resulting in the formation of 8 cells. Egg, synergids, and antipodals are well marked by their positions (fig. 8). After fertilization the endosperm develops rapidly, and soon fills the embryo sac with a mass of firm, heavy-walled tissue (fig. 9), after which the division of the fertilized egg produces the usual form of proembryo (fig. 10). The ultimate fate of the endosperm in this species is not known.

4. Philodendron Wendlandii

The staminate flowers crowd the upper part of the slender spadix and consist each of a single, 4-loculate stamen without floral envelopes. Dehiscence is along longitudinal grooves. The divisions of the mother cells are simultaneous, producing the usual type of tetrad. The tapetum is rather thin (3–4 layers of cells) and breaks down early, the nuclei sometimes floating free for a time before complete disintegration takes place.

Nine carpels are arranged radially around a common axis, forming a single compound pistil. Each carpel contains two slender pseudo-anatropous ovules. It is probably correct in this case to regard the placenta as the suppressed floral axis and the ovules as lateral shoots (fig. 11). The thin integuments project far over the tip of the nucellus, the lateral portion of which becomes sup-



FIGS. 7–10.—*Anthurium crystallinum:* fig. 7, four megaspores, the uppermost one of which functions; fig. 8, embryo sac, showing six of the eight cells; fig. 9, embryo sac filled with endosperm, the latter partially diagrammatic; fig. 10, egg-shaped proembryo.

FIGS. 11, 12.—*Philodendron Wendlandii:* fig. 11, ovule of peculiar reversed type found in this and a few other species; fig. 12, embryo sac with contents.

FIGS. 13–24.—*Xanthosoma* sp.: fig. 13, the 5 antipodals; fig. 14, egg apparatus; fig. 15, same in diagonal section of embryo sac; fig. 16, transverse section showing egg; fig. 17, polar nuclei about to fuse; fig. 18, nucleus of somatic cell in early prophase; figs. 19, 20, later prophases: figs. 21, 22, nuclei showing 16 chromosomes; figs. 23, 24, spindle.

pressed through the pressure of the growing embryo sac. The latter is 8-celled, the arrangement being of the usual type (fig. 12).

The endosperm is heavy-walled as in *Anthurium*, and the proembryo is egg-shaped.

5. Philodendron gloriosum

The ovule is much like that of the species just described. Like it the embryo sac is 8-celled, the endosperm is heavy-walled, and the embryo spherical to ovate.

6. Arum maculatum

This plant was obtained from a local florist and grown in pots. Owing to difficulty in the fixation of material the earlier phases cannot be given. It has the usual 8-celled embryo sac and spherical proembryo, and a thin-walled endosperm which is persistent in the seed.

7. Xanthosoma sp.

Through accident the label attached to this specimen was lost in transit. As the material was cut into cubes and in the fixing medium its identity could not be traced.

Each cell of the tricarpellate ovary contains two slender anatropous ovules. A series of long conducting cells lines the interior of each carpel and extends to the micropylar extremity of the ovule. The extremity of the truncate style is covered with glandular papillae. The ovule is extremely slender, as in *Philodendron*, but is sessile and does not occupy the reversed position. There appear to be 5 antipodals (fig. 13), the other contents of the embryo sac being what might be anticipated in any angiosperm (figs. 14–17).

Many of the cells surrounding the embryo sac were found to be in an active state of division, probably owing to the increase necessitated in the accessory tissue by the enlargement of the embryo sac. This gave a good opportunity to study the phases of homotypic division. No continuous spirem stage could be discovered. The chromatin reticulum is at first very fine, the strands later shortening and thickening, and finally breaking into an irregular mass of coarse threads which soon resolve themselves definitely into 16 chromosomes. Early splitting of the chromosomes was noticed in a few cases (figs. 18–24).

Homalomena argentea

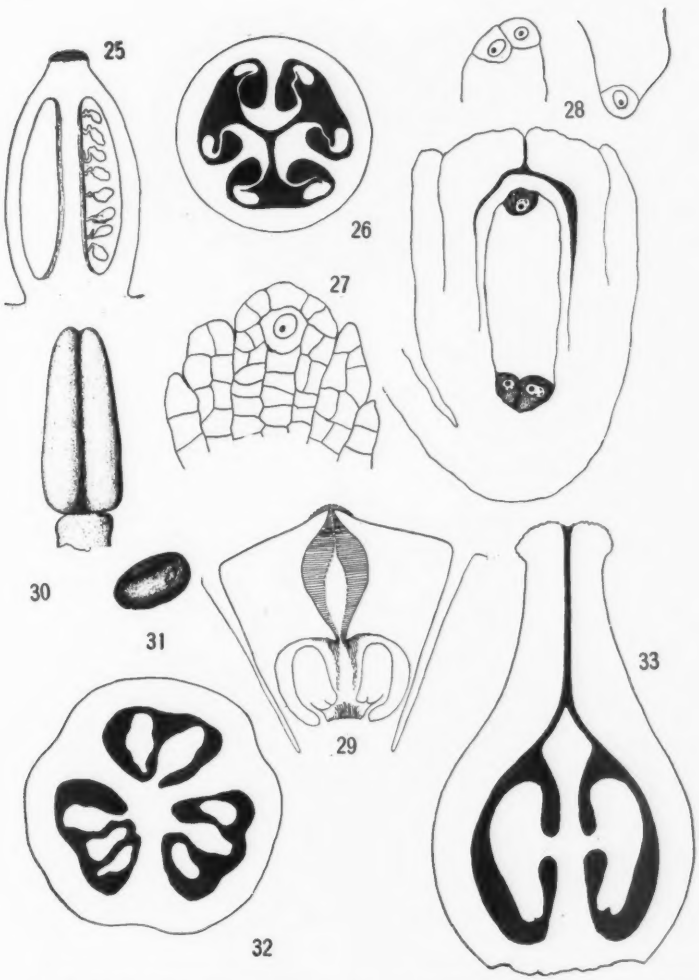
The lower part of the cylindrical spadix is crowded with the pistils, interspersed with numerous staminodia; the upper is crowded by the equally numerous stamens. Each pistillate flower consists of a single ovary, which in turn is made up of 3 foliaceous carpels. The ovules spring from the infolded edges of the placentae, and are arranged in 6 ranks (fig. 26). There is no open stylar canal, but the inner tissues of the style are loose and spongy (fig. 25). The anatropous ovule is mounted on a slender funiculus. When it has fully developed, the inner integument is massive and closes over the tip of the nucellus (fig. 28). The outer remains as shown in the figure.

The primary archesporial cell is somewhat larger than the surrounding cells (fig. 27). It divides once transversely, and of the two resultant cells the outer one functions, the inner one being broken down and absorbed. Whether the latter is to be regarded as one of a "row of two" or as a vestigial tapetum is purely an academic question. Functionally it is a tapetal cell. The embryo sac contents consist of the usual 8 cells arranged in the typical manner (fig. 28).

9. Stenospermation popayanense

A curious anomalous form was found in the Botanical Gardens under the name *Stenospermation pompayanense*. This may be a monstrosity, but of such a sort that its description should be of interest, and may have some morphological significance. Only one plant was found, and it bore no staminate flowers, and apparently no normal stamens, although *Stenospermation* is described by SCHOTT as having hermaphrodite flowers, with "stamina quattuor, singulo pistillo annexa." It may be, therefore, that this is not a member of the genus *Stenospermation*, although so labeled. The specific name *pompayanense* is an old synonym of the original name *popayanense*.

In the form under discussion, whatever its real identity, the long slender spadix is covered with lozenge-shaped blossoms which remind one at first glance of the closed blossoms of *Symplocarpus foetidus*. The resemblance is purely superficial. In *Symplocarpus*



FIGS. 25–28.—*Homalomena argentea:* fig. 25, longitudinal section of ovary; fig. 26, transverse section of ovary; fig. 27, primary archesporial cell; fig. 28, embryo sac with six of the eight cells.

FIGS. 29–31.—*Stenospermation popayanense* (?): fig. 29, vertical section of carpel, showing ovules in position, and the stylar canal filled with conducting cells; fig 30, stamen in cavity of pistil; fig. 31, pollen grain.

FIGS. 32, 33.—*Richardia africana:* fig. 32, transverse section of ovary, showing position of ovules; fig. 33, longitudinal section cutting two ovules.

the lozenge is formed by the infolded edges of the floral envelopes, while the central projecting "button" is produced by the protrusion of the anther tips. In the so-called *Stenospermation* the lozenge is merely the smooth upper surface of the thick-walled carpel, and there are no floral envelopes and no stamens surrounding the carpel. The "button" is the projecting stigmatic area (fig. 29). In the cavity of the carpel are found a circle of 4–8 erect anatropous ovules. Owing to the hardening of the gum contained in the tissues of this plant (and which resisted all reagents), sections could not be cut in paraffin, and the internal structure of the ovule cannot be described. Rather thick sections of the carpel were cut in celloidin, showing details of the stylar canal, and the curious crowded conducting cells as figured.

While all the blossoms are alike so far as outward appearance is concerned, a certain number of them (about 40–50 per cent) are found to bear stamens in place of the ovules just described. They are arranged in a circle, similar to the arrangement of the ovules, have large, well developed anthers with a broad connective, and when examined appeared about ready for dehiscence. The filaments of course are extremely short. If they lengthen later, no suggestion of such lengthening appeared in the material under examination. The exterior appearance of the "ovary," if such it may be called, is exactly the same whether it contains ovules or stamens. When torn open and mounted in glycerin, the anthers were seen to be filled with matured and normally formed pollen grains. No extra-carpellary stamens were found. The staminate carpels (if such they may be called) were found mixed among the pistillate, but somewhat more numerous toward the upper end of the spadix. In a very few cases the same carpel was found to house both stamens and ovules.

10. Arisaema triphyllum

The embryogeny of this species has been already discussed.[2] For the investigation of the microsporangium bulbs were collected in September and the blossoms dissected out. It was found that

[2] GOW, JAMES ELLIS, Embryogeny of *Arisaema triphyllum*. BOT. GAZ. **45**:38–44. *figs. 24.* 1908; also MOTTIER, DAVID M., On the development of the embryo sac of *Arisaema triphyllum*. BOT. GAZ. **17**:258–260. *pl. 18.* 1892.

the entire microsporangial structure was fully matured at that time; the mother cells had disappeared and the pollen grains were found lying free in the loculi of the anther. Almost all the bulbs were such as had borne pistillate blossoms the preceding season; in fact the material was collected after the early frosts and was discovered by means of the conspicuous clusters of bright red berries after the withering of the leaves. A very few of the bulbs were laterals formed from the central bulb during the growing season. Two or three of the bulbs collected contained a monoecious spadix. Two-thirds of the balance contained staminate blossoms only. *Arisaema* seldom bears staminate and pistillate flowers on the same spadix, but the indication is that the plant that bears pistillate flowers one year bears staminate flowers the next. It is, in a way, consecutively monoecious, seldom simultaneously monoecious.

The loculi of the stamens contained many normal pollen grains, but far more small suppressed grains, the ratio being about 2:1, suggesting the inability of the plant to muster sufficient energy to mature all the pollen it produces.

11. Richardia africana

This plant, the *Calla aethiopica* of the florists, was found in every stage of development at the Cedar Rapids greenhouses, and fixation proved extremely easy owing to the absence of mucilage in the tissues.

The upper portion of the slender spadix is covered by a densely crowded mass of stamens, while the pistillate flowers occur below. SCHOTT describes the pistils as "organis neutris tribus cincti," but in perhaps a fourth of the blossoms these "neutral organs" turn out to be functioning stamens, while in the remainder they are staminodia, or staminal rudiments.

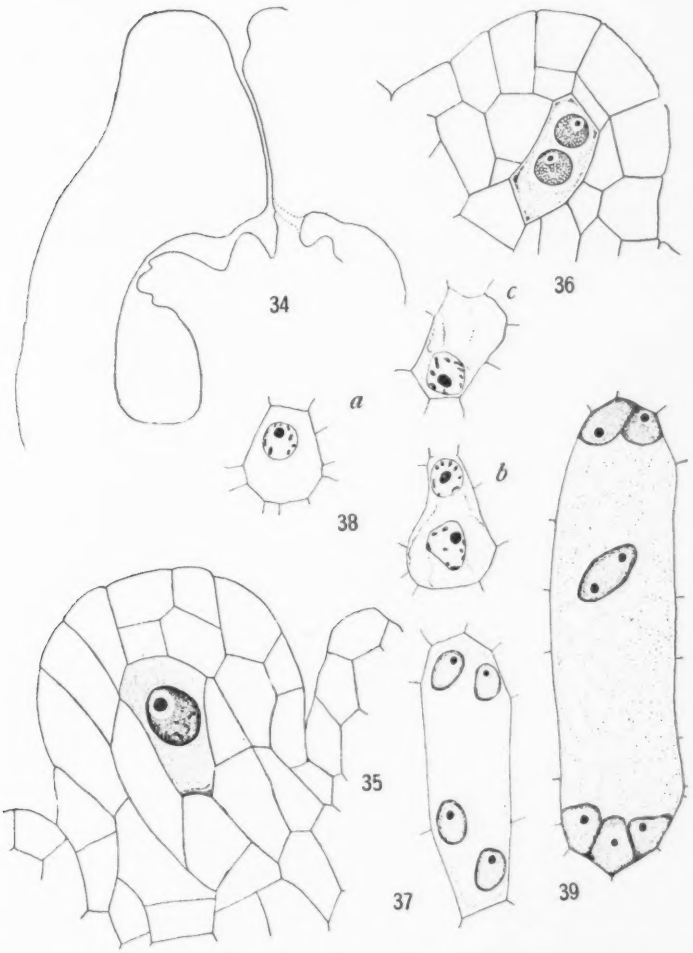
The cylindrical ovary consists of 2, 3, or 4 carpels, the anatropous ovules being borne on the central placenta, which here represents the united carpellary walls. Two to four ovules occur in each carpellary cavity (fig. 32), and a separate branch of the open stylar canal runs to each cavity. The ovule is anatropous, and of foliar origin, since it springs from the carpellary wall. The

funiculus is laterally attached. There are the usual two integuments, which grow well out beyond the tip of the nucellus (fig. 33). The ovule first appears as a lateral projection nearly filling the cavity of the immature carpel. As the latter enlarges, the ovule keeps pace with it. The integuments begin to appear before it assumes the anatropous position (fig. 34). The primary archesporial cell is differentiated about simultaneously with the appearance of the integument, and even in its resting condition may be recognized by its greater size (fig. 35). After, or simultaneously with, its differentiation, the tip cells of the nucellus divide by periclinal walls, forming two cell layers outside the archesporium. No primary parietal cell is formed. The primary archesporial cell is in this species the spore mother cell, and develops directly into an embryo sac without the previous formation of a row of megaspores. The first division occurs early (fig. 36). The later divisions follow in the usual order (figs. 37–39), and before their completion the integuments have reached complete maturity, closing over the tip of the nucellus.

The account just given represents the normal development of the ovule and embryo sac in *Richardia* and holds true in perhaps 5 per cent of the plants examined. In most cases, however, the plants not only fail to set their seed, but will not do so even when artificially pollinated. I refer here solely to the plant as I have observed it growing in local greenhouses, and to the individuals (some 150) on which I have tried the experiment of artificial pollination. The observation of gardeners, so far as they have been consulted, confirms the conclusion that the vast majority of plants of the strains here cultivated, and under the conditions existing in local greenhouses and gardens, cannot be made to produce seed. BURBANK, on the other hand, reports that the *Richardia* as it grows wild in California matures seed in great abundance.[3]

The behavior of the artificially pollinated ovaries is peculiar. Ovaries not artificially pollinated shrivel in 10–15 days after reaching maturity. Pollinated ovaries behave otherwise. A large

[3] "The calla lily, in all its varieties, blooms and seeds in the utmost profusion here in California, setting big plump seeds in abundance. This includes all the yellow, white, and black varieties. I think the cause of not setting seeds in the east is wholly climatic."—From a private letter addressed to the writer.



FIGS. 34–39.—*Richardia africana:* fig. 34, immature carpel, containing developing ovule which is just beginning to show the anatropous character; fig. 35, primary archesporial cell; fig. 36, first nuclear division in formation of embryo sac; fig. 37, four-nucleate embryo sac; figs. 38, 39, mature embryo sac.

number of flowers were pollinated early in January. Three weeks later the ovaries had swollen to the size of large peas, and the gardener—a veteran in the growing of the *Richardia*—was confident that seed would be set. Within the following week most of these had begun to wilt, but a very few continued to grow until they were as large as small hazel nuts. Within two weeks almost all were withering, and from then on the molds rapidly made away with them. Five per cent or less of the pollinated plants produced seed.

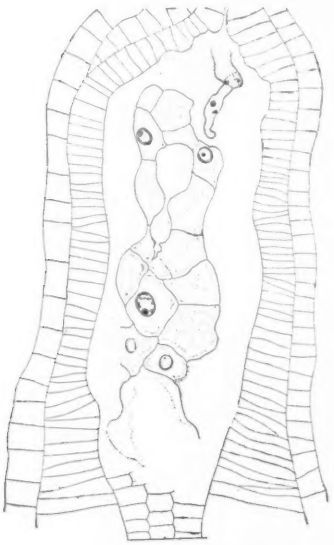


FIG. 10.—*Richardia africana:* disintegrating sterile nucellus and tip of pollen tube.

The explanation of this behavior is to be found in the fact that the greater number of ovules are congenitally sterile and develop no embryo sac. In some cases no cell can be discovered that can be definitely identified as a primary archesporial cell. In other cases it would seem that a potential archesporial cell makes its appearance, but fails to complete its normal course of development. The latter is to be inferred from the fact that the number of primary archesporial cells encountered in the very young material vastly exceeds the number of embryo sacs in the more mature material.

Sections of pollinated pistils containing sterile ovules demonstrated the fact that, in some cases at least, the pollen tube penetrates a sterile ovule, and reaches the tip of the nucellus. The fact that the pollinated sterile ovaries reach a considerably higher stage of development before withering than do unpollinated ovaries of the same sort would appear to be due to the stimulus of pollination. At all events, the writer can find no other cause to which it can reasonably be attributed. The direction of the pollen tube

into the ovule is probably determined by the presence of nutritive material in that quarter, since the nucellar cells, and even the tip cells of the integuments often become somewhat swollen and glandular and break down readily. If this be the case, the tube should enter a sterile ovule quite as readily as a fertile one. In a number of cases remains of shrunken pollen tubes were observed near or in contact with sterile nucelli (fig. 40).

The sterile nucellus finally breaks down, the process usually beginning within, and sometimes resulting in, the formation of an interior cavity before the disintegration of the outer cells (figs. 40, 41), and the nuclei of the cells occasionally lie free in this cavity before disintegration. The breaking down of the nucellus finally leaves the cavity within the integuments completely empty; the ovule soon collapses and begins to decay.

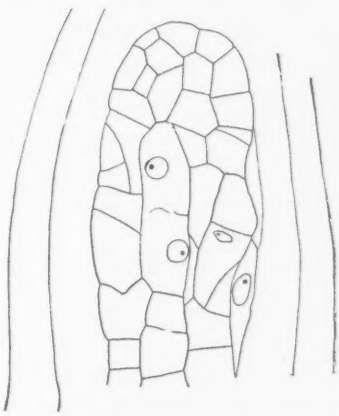
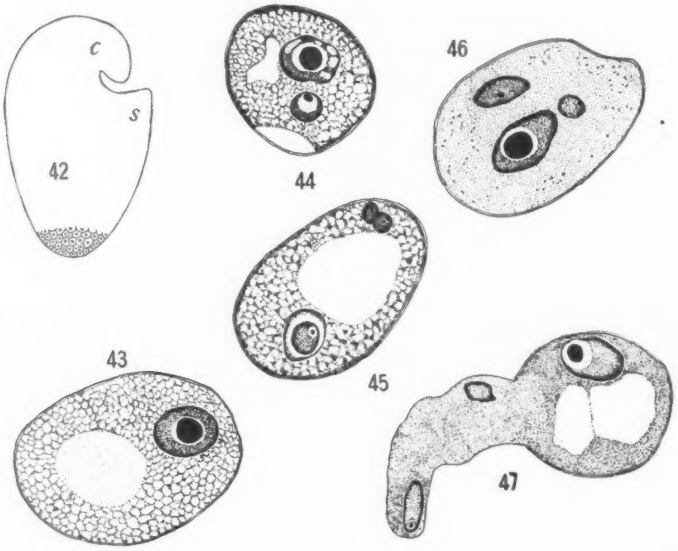


FIG. 41.—*Richardia africana:* sterile nucellus; disintegration just beginning.

In the case of fertile ovules, the embryo sac is of the usual 8-celled type. The cavity soon becomes filled with a mass of thick-walled endosperm cells, and the endosperm is persistent in the seed. The proembryo develops a little later than the endosperm, and is spherical in shape, finally lengthening out and developing a distinct notch (fig. 42).

Anthers dissected out, before the appearance of the flower bud as a swelling under the leaf-sheath, disclosed many large multinucleate mother cells. Tetrads are formed by successive divisions, the 4 daughter cells lying in the same plane. Material taken from a plant in which the flower bud was beginning to form a prominent swelling within the stem disclosed mature pollen grains filling the loculus of the anther. The latter has the usual thickened epidermal layer of rather small cells, inside which is an endothecium of large cylindrical cells with riblike thickenings. The tapetum consists

of a layer 3 cells deep and disintegrates early. The spores lie in a mass of gelatinous material, the remains of the former tapetum, and scattered among them are many small, ill developed cells which show a tendency to break down. These are abortive pollen grains, or possibly in some cases abortive mother cells.



FIGS. 42–47.—*Richardia africana:* fig. 42, embryo in early stage of development; *c*, cotyledon; *s*, stem tip; fig. 43, mature pollen grain previous to nuclear divisions; fig. 44, pollen grain previous to division of generative cell; fig. 45, male cells in contact; fig. 46, tube nucleus and male cells, the latter abnormal as to shape and comparative size; fig. 47, sprouting pollen grain.

There is a great lack of uniformity in the divisions within the pollen grain. In one case (fig. 43) all were delayed until after dehiscence; but this is certainly very unusual. The first nuclear division, by which the generative nucleus is differentiated, usually occurs early. The generative nucleus does not surround itself with cytoplasm and a distinct cell membrane, but retains its nuclear character after division. Usually it divides before dehiscence occurs (fig. 45), although a number of grains were taken from

dehiscing anthers in which it was found that this division had not yet taken place. Grains were sprouted in weak solutions of glucose and lactose, and examined unstained, or stained in a weak aqueous solution of hematoxylin. One of these is indicated in fig. 47.

Summary

1. The development of the archesporium in aroids follows no uniform rule. In one species studied,[4] the primary archesporial cell produces two megaspores, the outer one of which functions; in two cases there are four megaspores, the outermost one of which functions; in one case the primary cell produces two cells, one of which may be a tapetal cell; one species develops four megaspores in the same horizontal plane, and the functioning one then develops a tapetal cell at its upper end; one species develops four megaspores, the innermost of which functions; and in one case the primary sporogenous cell develops directly into an embryo sac.

2. The number of antipodals varies from 3 to 11, four species having regularly more than 3. This is a relatively primitive feature, and occurs in other primitive orders.

3. Previous to the work here reported, embryos of the spherical type lacking a suspensor had been reported by CAMPBELL in *Pistia*, *Dieffenbachia*, and *Lysichiton*. The writer has confirmed CAMPBELL'S observation with regard to *Dieffenbachia*, and has discovered the same sort of embryo in *Nephthytis*, *Philodendron*, *Arum*, *Aglaonema*, *Anthurium*, *Arisaema*, *Symplocarpus*, and *Richardia*. It seems clear that this type of embryo is characteristic of this family.

4. *Richardia* as here cultivated in the greenhouse has usually a sterile nucellus and does not develop an embryo sac. The disintegrating nucellar cells act as conducting tissue, and the pollen tube enters sterile nucelli, although gametic attraction cannot exist. The direction of the tube is conditioned on the presence of nutritive material.

5. Reduction of parts is indicated by the presence of staminodia in several of the species studied.

6. In an abnormal specimen supposed to belong to the genus

[4] GOW, JAMES ELLIS, Studies in Araceae. BOT. GAZ. **46**:35–42. *pls. 4–6.* 1908.

Stenospermation functioning stamens replace the ovules in many of the carpellary chambers. This reminds one of a somewhat similar abnormality noted by CHAMBERLAIN in *Salix*, and of characteristics noted by TREUB in *Balanophora* and *Loranthus*.

7. In three species investigated with regard to number of chromosomes the homotypic number was found to be 16.

8. Tetrad formation in the anthers of some species is by means of simultaneous, in others by successive, divisions.

9. In *Richardia* the male nuclei are not surrounded by a definite cytoplasmic envelope, and the division producing them is often delayed until dehiscence or later. Sometimes the earlier divisions are similarly delayed.

10. The bulb of *Arisaema* may bear staminate and pistillate blossoms in alternate years.

Thanks are due to Mr. FRED J. SEAVER, of the New York Botanical Gardens, for furnishing most of the material on which the foregoing observations were made. The author also wishes to express his deep obligation to Professor T. H. MACBRIDE, of the State University of Iowa, for the suggestion which first led to the undertaking, and for advice and assistance freely rendered at every stage of the work.

CEDAR RAPIDS, IOWA

SUMMER EVAPORATION INTENSITY AS A DETERMINING FACTOR IN THE DISTRIBUTION OF VEGETATION IN CONNECTICUT

GEORGE ELWOOD NICHOLS

For an area of its size, the state of Connecticut exhibits considerable diversity both in topography and in vegetation. From a geographical standpoint three well defined regions may be recognized: the Western Highland, the Eastern Highland, and the Central Lowland. The surface of the Highlands is for the most part exceedingly rugged, and in the northern part of the state, especially in the Western Highland, elevations of 300 or more meters are common. The Central Lowland is characterized, on the whole, by its gentler contours and lesser elevations. Over large areas here the surface is almost level, while the hills, as a rule, seldom reach a height of more than 75 meters. Exception to this latter statement, however, must be made in the case of the trap ridges which traverse the Lowland from north to south, dividing it lengthwise into two sections. In topography these conform with the Highlands rather than the Lowland. Geologically, as well as topographically, the Highlands contrast sharply with the Lowland. Except for limited areas of limestone, the Highlands are underlain by granites, gneisses, and schists. The Lowland rocks are sandstones and shales. Throughout the state, however, the underlying rock is in large part covered over by a mantle of glacial drift which in places is more than 50 meters in thickness.

The vegetational differences between various parts of Connecticut are not so sharply or clearly defined. Moreover, the situation is complicated by the fact that practically the entire area at one time or another has been deforested, while a large share of it is at present under cultivation, so that the nature of the original plant covering has become more or less modified. Considering the vegetation of the state in its entirety, the ultimate climatic formation is a forest dominated by various deciduous trees and hemlock. Of the virgin forest scattered remnants are occasionally encountered, but for the most part the present woodlands are second growth.

These undoubtedly differ in many respects from the original forests. Nevertheless, it seems probable, due to the sprouting capacity of the majority of the constituent trees, that in favorable cases, except for a decrease in the proportion of hemlock and a corresponding increase in the proportion of chestnut, the general aspect of the forest has not greatly altered during the last three centuries. The composition of this forest, however, was never uniform throughout the state. In northwestern Connecticut the original forest was of the so-called Northern hardwood type. Here the dominant trees were sugar maple, beech, and hemlock, associated with which were yellow birch, chestnut, and other hardwoods. Just how large a portion of the state was originally clothed by this type of forest is uncertain, but it undoubtedly was present throughout the greater part of the northern half of the Western Highland and extended southward toward the shore of Long Island Sound. In all probability it was also characteristic of at least the northern portion of the trap range and of the northernmost section of the Eastern Highland. Along the coast and throughout the greater extent of the Central Lowland, so far as can be determined, the most widely distributed type of original forest was composed largely of chestnut and various oaks. The trees characteristic of the northern hardwood forest were also present here, but were relatively less abundant and more restricted in their occurrence. In the forests of this area the tulip tree was frequently an important component. The original forests of the Eastern Highland, except in the northernmost part, would appear to have resembled more closely those of the coast and Lowland than those of the Western Highland. In the present forests the prominent trees are the oaks, especially the white and the red oak. Chestnut, while present, is much less conspicuous than in the Lowland forests. Hemlock, beech, and maple are of subsidiary importance.

There are other important and even more striking vegetational dissimilarities between various parts of the state. The discussion of these, however, is reserved for papers in course of preparation, in which the plants of the state are to be considered from an ecological standpoint.[1] It was the primary object of the experiments

[1] The first paper of this series, "The vegetation of Connecticut I. Phytogeographical aspects," has already been published (Torreya **13**: 89–112. 1913).

to be described in the present paper to determine whether the distribution of the climax types of vegetation could in any way be coordinated with differences in the evaporating power of the air during the growing season. As is generally recognized, one of the greatest dangers that beset the growing plant is loss of water through transpiration. In ordinary plants, as soon as the amount lost in this manner exceeds that absorbed by the roots, the plant wilts. The rate at which transpiration goes on in any particular plant is regulated largely by the evaporating power of the surrounding air, and this in turn is dependent upon a complex of factors, such as humidity, temperature, direction and velocity of wind, etc. When exposed to uniform atmospheric conditions, however, it is known that the rate at which water is transpired by different kinds of plants varies, mesophytes transpiring more rapidly, xerophytes more slowly, and so on. That the great centers of plant distribution in various parts of the United States are directly related to well marked differences in the summer evaporation intensity has been ably demonstrated by LIVINGSTON,[2] while the earlier work of TRANSEAU[3] indicated an analogous correspondence between the precipitation-evaporation ratios for the entire year and forest distribution. It seemed possible, therefore, that in the area under consideration similar relations on a smaller scale might be detected.

Accordingly, with this object in view, during the summer of 1912 continuous evaporation records were taken at numerous localities in the state by means of porous clay cup atmometers of the type devised by LIVINGSTON.[4] For assistance in carrying out these experiments the writer is indebted to the various cooperators named below. The expense necessarily involved was in large part defrayed by Yale University. Altogether, 16 more or less widely separated stations were selected, and these were fairly uniformly distributed, through the three geographical regions of the state, 7 being located in the Western Highland, 3 in the Central Lowland, and 6 in the Eastern Highland. Three of the stations, one in each geographical region, were situated near the coast. The writer personally selected the sites and installed the atmometers at all the stations except

[2] Plant World **14**: 205–222. 1911.

[3] Amer. Nat. **39**: 875–889. 1905.

[4] Carnegie Inst. Publ. no. 50. 1906.

Storrs and Haddam. So far as possible, the sites were made to conform with one another, the instruments being placed in the open, where they would be freely exposed to the action of both sun and wind. Brief comment regarding the nature of the respective sites, together with the names of the various observers, is given in the following paragraph.

WESTERN HIGHLAND.—Salisbury: open hillside, north exposure, altitude 210 m.; Mrs. CHARLES S. PHELPS. North Colebrook: open field, slightly shaded in early morning and late afternoon, altitude 224 m.; station of particular interest on account of proximity to large tract of virgin northern hardwood forest; Mr. CARRINGTON PHELPS. West Cornwall (Cream Hill): hillside, west exposure, slightly protected from wind by trees, altitude 390 m.; Mr. C. L. GOLD. Litchfield: lawn in proximity of buildings, altitude 330 m.; Rev. JOHN HUTCHINS. Hawleyville: hillside lot, west exposure, slightly shaded in early morning and late afternoon, altitude 156 m.; Mr. C. B. HAWLEY. Collinsville: hillside lawn, west exposure, buildings in vicinity, altitude 135 m.; Mr. G. J. CASE. CENTRAL LOWLAND.—Hayden: open field, altitude 15 m.; site typical for neighboring tobacco plantations; Misses HELEN and GRACE CLAPP. Southington: lawn, in proximity of building; altitude 45 m.; Miss EUNICE MACKENZIE. EASTERN HIGHLAND.—Haddam: hill crest, altitude 144 m.; Professor A. L. DEAN. Storrs: open hillside, west exposure, altitude 195 m.; Professor L. A. CLINTON. Colchester: hillside cemetery, slightly shaded in late afternoon, east exposure, altitude 150 m.; Mr. H. P. BUELL. Danielson: hillside, west exposure, altitude 75 m.; Mr. F. E. BITGOOD. Voluntown: hill crest, altitude 82 m.; Mr. J. L. HERBERT. COASTAL REGION.—Niantic: lawn, in proximity of trees and buildings, slightly shaded in early morning, within 90 m. of sea shore, altitude 5 m.; Mrs. F. H. DART. New Haven: open lawn, slightly protected from wind, about 3 km. from shore, altitude 18 m.; G. E. N. Westport: hillside, about 0.5 km. from shore, altitude 30 m.; Mr. GRENVILLE MACKENZIE.

In each of the above mentioned localities a pair of atmometers was installed side by side, about 50 cm. apart. The bottles to which the cups are connected were set upon a T-shaped wooden support, being held in position by zinc casings made for the purpose. The base of the cup itself was thus raised about 56 cm. from the ground, or high enough to insure free circulation of the air about it. The entire apparatus was inclosed within a coarse-meshed chicken-wire cage. Of the two cups installed at the beginning of the season at each station, one was replaced by a fresh one after an interval of 5 weeks; the second original cup was renewed at the end of 10

weeks; and 5 weeks later a fourth cup was substituted for the one which at that time had been longest in operation. Distilled water was used in all cases. The majority of the instruments were set up during the last week of May and continued in operation until September 14. At the end of the season the cups were returned to the writer and restandardized,[5] the readings being then corrected in the usual manner,[6] and all results coordinated with those derived from standard cups. Except where for one reason or another particular cups were manifestly unreliable, the records of the two were averaged to obtain the accepted readings.

In this way a practically complete set of weekly readings throughout the season has been tabulated for nearly every station. Such a series of figures brings out a number of interesting facts. It is found that for the state as a whole the maximum weekly rate of evaporation for the season occurred during the first week in July, when there was an average water loss from each cup of 211 cc. During this week the instruments at Hayden evaporated 256 cc., and at 5 other inland stations in the Lowland and Eastern Highland the rate exceeded 225 cc., while at Niantic there was a loss of but 144 cc. At no time during the season did the amount evaporated during the recorded week at any of the stations in the Western Highland or in the Coastal Region amount to as much as 225 cc. The lowest rate of evaporation throughout the state was observed during the first week in September, when the average was 41 cc., the minimum being reached at Niantic (22 cc.). The mean weekly evaporation rates for the state as a whole, based on the averages of all the stations, were as follows:

June	1	June	8	146 cc.	July	27–Aug. 3	121 cc.
"	8– "		15	178 "	Aug.	3–Aug. 10	113 "
"	15– "		22	124 "	"	10– " 17	108 "
"	22– "		29	153 "	"	17– " 24	53 "
"	29–July		6	211 "	"	24– " 31	125 "
July	6– "		13	155 "	"	31–Sept. 7	41 "
"	13– "		20	119 "	Sept.	7– " 14	104 "
"	20– "		27	170 "			

[5] See NICHOLS, G. E., A simple revolving table for standardizing porous cup atmometers. BOT. GAZ. **55**: 249–251. 1913.

[6] See Plant World **13**: 111–115. 1910.

There seems to be no obvious advantage, so far as general considerations are concerned, in setting forth in detail the results for each week in each locality. It has rather seemed simpler to give local averages for longer periods, a method already adopted by LIVINGSTON[7] in presenting similar data. The periods selected correspond approximately to the three summer months—June, July, August—and the first half of September. The mean weekly evaporation rates for the various stations during these periods are given in table I.

TABLE I

MEAN WEEKLY EVAPORATION RATES IN CC., AS RECORDED BY THE POROUS CUP ATMOMETER, FOR 16 STATIONS IN CONNECTICUT, FROM JUNE 1 TO SEPTEMBER 14, 1912. FIGURES IN PARENTHESES INDICATE NUMBER OF WEEKS FOR WHICH READINGS ARE RECORDED, IF LESS THAN THE STATED PERIOD

Station	June 1 to June 29	June 29 to Aug. 3	Aug. 3 to Aug. 31	Aug. 31 to Sept. 14	Average for season	June 1 to Aug. 3
Salisbury	152	168	109	69	134	161
Colebrook	133 (2)	119	87	53	100 (14)	122 (7)
Cornwall (Cream Hill)	115	130	79	65	103	123
Litchfield	113	147 (4)				130 (8)
Hawleyville	119	141	113	89	121	131
Collinsville	144	161	98	71	128	154
Hayden	165	182	124	77	148	174
Southington	170	167	109	70	140	168
Haddam	197	184	99	67	149	189
Storrs	182	175	100	97	146	178
Colchester	157	156	99	79	131	157
Danielson	181	173	100	101	143	172
Voluntown	176	165	112	81	143	170
Niantic	104	105	71	40	87	104
New Haven	146	145	102	68	123	146
Westport	142	165	107	71	134	156

In considering the evaporation intensity of the air as a possible factor affecting the distribution of the vegetation in this region, it seems reasonable to assume that its effect on plants is felt most keenly during the earlier part of the growing season, at a time when growth and development are taking place most rapidly and when the immature tissues and organs are as yet inadequately protected from excessive transpiration. An examination of the first four

[7] Plant World **14**: 205–222. 1911.

columns of figures in table I reveals the fact that during the first two monthly periods the mean weekly rate of evaporation far exceeded that maintained during the latter part of the season. In other words, the period of maximum evaporation coincided approximately with the more critical period of vegetative activity. In view of this correlation, coupled with the natural assumption that it is the periods of excessive evaporation that are most influential in determining the character of vegetation, it has been thought best in drawing conclusions to disregard entirely the data obtained during the latter part of the season, when for the most part a uniformly low rate of evaporation prevailed throughout the state, and to base deductions on the observations of these first two months. The mean weekly rates of evaporation obtaining at the various stations from June 1 to August 3 have therefore been indicated in the last column of table I. With these figures as a basis, it is a simple matter to compute approximately the relative evaporating power of the air for the various geographical and vegetational regions of the state during the period of combined maximum vegetative activity and evaporation intensity for the year 1912. Upon averaging the results for the inland stations of the Highlands and Lowland and of the stations along the coast, it is found that the weekly water loss, as recorded by the porous cup atmometer, was as follows: Western Highland, 137 cc.; Central Lowland, 171 cc.; Eastern Highland, 173 cc.; Coastal Region, 135 cc. It would thus appear that the area dominated largely by the mesophytic northern hardwood type of forest, and the strip along the coast, constitute areas of relatively low evaporation intensity; and that the rate of evaporation in the Eastern Highland, where oaks predominate in the forest, is somewhat higher than that in the Central Lowland, where the more mesophytic chestnut is the character tree. The relatively low evaporation rate along the coast was not wholly unexpected and will be referred to again. Explanation for the gradual diminution in evaporation intensity apparent in passing from west to east along the coast may be looked for in the fact that while the western part of the shore is shut off from the ocean by Long Island, the eastern portion is more exposed and therefore possesses a more maritime climate.

In the foregoing paragraphs no account whatever has been taken of the varying amounts of precipitation occurring in different sections of the state. But since the amount of water present in the ground and therefore available for plant use is in itself a potent factor in determining the character of vegetation, and since its abundance is so largely controlled by the amount of precipitation, it is necessary, in order to gain a comprehensive view of the situation, that the relationship between the phenomena of precipitation and evaporation within the area under discussion be considered. So far as observed, there is no constant ratio between the rate of precipitation and the intensity of evaporation. Thus the rate of evaporation during a heavy rain is hardly lower than during a dense fog. But the ratio between the *amount* of precipitation and that of evaporation, especially over considerable periods of time, is of vital significance. In the state of Connecticut there is an average annual precipitation of 120.9 cm. (47.59 inches).[8] This is distributed approximately as follows: Western Highland (inland), 126.8 cm. (49.94 in.); Central Lowland (inland), 119.6 cm. (47.08 in.); Eastern Highland (inland), 117.7 cm. (46.35 in.); Coastal Region, 116.8 cm. (45.98 in.). Of more special interest, however, for the purpose of comparison with the observed rates of evaporation, are the amounts of rainfall that occurred in the various localities during the past season for the period extending from June 1 to August 3. These, together with the contemporaneous evaporation records, are therefore indicated in table II. For convenience in comparing the two sets of data, the evaporation readings, heretofore given in terms of cc., are here expressed in units of depth as well, the conversion being made with reference to a more or less arbitrarily chosen free water surface.[9]

An examination of table II shows very convincingly that, for the period under observation, nowhere in the state would the amount of rainfall have compensated for the amount of water which would have been evaporated from a free water surface during

[8] Based on records from 14 scattered stations. This and the following figures regarding precipitation have been computed from statistics published in the *Monthly Weather Review* of various dates.

[9] The standard water surface on which these reductions are based is that used by LIVINGSTON (see Plant World **14**: 214, 215. 1911).

the same interval. As is indicated in the last column, the disparity was least in the Western Highland, greatest in the Eastern Highland. The fact that, despite this at first sight rather startling deficiency in precipitation as compared with evaporation during this particular season, plants were still able to maintain the balance between absorption and transpiration may be attributed partly to the manner in which evaporation is modified by the physical structure of various soils, partly to the adequacy of the ground-water supply, which in turn is largely dependent on the influx of water

TABLE II

MEAN WEEKLY RATES OF RAINFALL AND EVAPORATION DURING THE PERIOD OF 9 WEEKS FROM JUNE 1 TO AUGUST 3, 1912

	MEAN WEEKLY RAINFALL		MEAN WEEKLY EVAPORATION			RATIO BETWEEN RAINFALL AND EVAPORATION
	cm.	in.	cc.	cm.	in.	
Western Highland..	1.19	0.47	137	1.94	0.76	0.61
Central Lowland...	1.14	0.45	171	2.42	0.95	0.47
Eastern Highland ..	1.02	0.40	173	2.45	0.96	0.42
Coastal Region.....	0.91	0.36	135	1.91	0.75	0.48

at times of the year when the effects of evaporation are less pronounced, and partly to various structural peculiarities of the plants themselves by which transpiration is regulated. Nevertheless, the marked excess in the rate of evaporation over that of precipitation at such a critical period in the life of the plant cannot but make some impress on the character of the vegetation. Another interesting fact is brought out in this table. As has already been noted, the absolute amount of evaporation in the Coastal Region is even lower than that in the Western Highland. But taking the ratio between the amount of evaporation and that of rainfall as a criterion, it is seen that conditions in the Coastal Region approximate more closely those in the Central Lowland. Similarly the less mesophytic nature of the Eastern Highland is forcibly accentuated.

It is fully appreciated that too definite conclusions cannot be drawn from such a series of experiments conducted for but a single season. It is recognized, furthermore, that it is well-nigh impossible to select with certainty in different localities representative sites

in which the instruments will be exposed to absolutely parallel atmospheric conditions. The danger in placing too much reliance on a single set of data for a given locality was impressed upon the writer by results secured from a supplementary series of instruments which was operated in various plant habitats in the vicinity of New Haven for the last five weeks of the season. During this period the mean weekly evaporation rate at the central station averaged 86 cc. Instruments in the other sites averaged as follows: exposed summit of trap ridge, about 6 km. from coast, altitude 81 m., 138 cc.; salt marsh, 128 cc.; lee of low sand dunes along shore, about 100 m. removed from salt marsh station, about 131 cc.; open bog, altitude 6 m., 81 cc. More accurate conclusions as to the evaporation intensity prevailing throughout the state might of course be derived from a series of instruments placed in diverse habitats in each of the localities selected and operated for several seasons, but at the present time no further investigation along these lines is contemplated. And while the data obtained from the experiments of this one season do not permit final conclusions, they at least suggest that the evaporation intensity of the air may be a factor of no little import in determining the character of the vegetation in different parts of Connecticut.

YALE UNIVERSITY

CURRENT LITERATURE

BOOK REVIEWS

Soil acidity

The injury to vegetation by smoke from factories and smelters is well known. Much has been written on the subject, and considerable experimental work is now under way in various parts of the world. WIELER[1] has published recently an account of one series of experiments, begun in 1905, dealing with plant growth and the lack of lime in the soil. In this account he defends the thesis that smoke and smelter fumes are injurious to plants, not because of their direct effect on the leaves, but because the acid-forming substances they contain are absorbed in the soil and there neutralize the lime so necessary to plant growth. He argues also that there is an injurious effect on the micro-organisms of the soil.

The region studied in greatest detail is a part of the Innerste Valley where considerable damage has been done by fumes from the Frankenscharrn smelters. The forest here has been driven back to considerable distances, amounting to 3.5 kilometers in some directions. Even where trees were still standing, they showed by their stunted appearance and yellow leaves or needles the injurious effects of conditions surrounding them. Certain slopes bore only heath, low shrubs, and stunted trees, others only grasses, and still others no vegetation at all. Injury was greatest close to the smelter and decreased as the distance from the smelter increased.

On the three kinds of slopes just described, experimental plots were laid out at distances of 0.5 to 1.5 kilometers from the source of the fumes. To these plots additions were made of lime, lime and ammonium hyperphosphate, and ammonium hyperphosphate alone. This substance was added on the supposition that the soil was poor in nitrogen. No striking results were obtained by its use, however, and it need not be considered further. Slaked lime was applied in finely ground form in quantities varying from 50 to 100 kilograms per hectare. Untreated plots were studied as checks in all cases.

Plantings were made of *Picea excelsa*, *Pinus sylvestris*, *P. montana*, *Quercus robur*, *Fagus sylvatica*, *Betula alba*, *Vicia villosa*, and *V. sativa*. It was found in all cases that plants on unlimed plots grew much less rapidly and appeared less healthy than those on limed plots. Conifers and legumes either did not grow at all without lime, or only poorly. Oak, beech, and birch proved to be less rigorous in their requirements, but did better on treated plots. Plants from seed gave poorer results than those transplanted from the nursery.

[1] WIELER, A., Pflanzenwachstun und Kalkmangel im Boden. 8vo. pp. vii+235. *figs.* 43. 1912.

Mention was made above of the yellow color of leaves on plants in affected areas. This condition is generally considered to be due to a lack of nitrogen in the soil; this in turn is a consequence of poor development of the bacterial flora. That such conditions prevail in the soil of these denuded or partly denuded hillsides was shown by the fact that in unlimed plots very few bacterial nodules were found on the roots of legumes. Development of such nodules was practically normal, however, where lime had been added.

Root systems were found to be small on unlimed soil. Both primary and secondary roots were short and there was only a small amount of branching. As a consequence, the whole root system formed a knob or lump which came in contact with very little soil and furnished poor anchorage for the plant. There was thus more danger of injury from drought and from strong winds. Results confirming those already described were obtained by liming soils in other localities, hence they need not be discussed here.

The author's idea of the causes of the deliming of soils and consequent inhibition of plant growth has already been stated. In a discussion of his results he considers these causes at some length. He finds, in the first place, that all the untreated soils really are poor in lime. Near the smelter this substance was present to the extent of 0.012 per cent; in experimental plots along the sides of the valley it varied from 0.017 per cent to 0.045 per cent; under a spruce stand it was 0.038 per cent.

Further investigation of these soils brought out the surprising fact that they were acid in reaction, instead of alkaline or neutral, as might have been supposed. It is known of course that wet moor soils are acid, but this has been found by BAUMAN and SULLY to be due, not to the presence of free humic acids, but to the power of certain substances in these soils to decompose salts by forcing acids out of combination and by absorbing the bases with which they were combined. These authors showed further that this reaction is brought about by the "absorptively unsaturated" condition of the cell walls of sphagnum. The acid character of moor soils depends, therefore, on the fact that the material from which they arise is already acid. But there is good reason, says WIELER, for thinking that dry peaty soils originate in the same way as do those of sphagnum bogs; that is, the plant remains in the former case are acid, just as they were in the latter. This deduction was amply confirmed by tests on living leaves and needles, the same organs dead and still remaining on the tree, or covering the ground beneath these trees.

That the acids set free in the manner indicated above are not neutralized or decomposed depends finally on the failure of microorganisms to do their usual work. From undecomposed organic remains acids are being washed out continually by rains. As soon as bacterial and fungal action begins these acids are broken up into harmless substances. In soils, however, where the acid content is steadily increasing, as in the region around the Frankenscharrn smelter, the bases, most important of which is lime, are neutralized. As a consequence, microorganisms do not thrive, and plant fragments and the soil

itself remain acid. And not only so, but the important process of nitrification, carried on by bacteria whose activity is closely connected with the amount of lime available, is seriously retarded. Leaves become yellow and there is a general nitrogen starvation of all vegetation.

It developed during the course of the investigation that the addition of lime to such soils, even though it improved materially the conditions for plant growth, reduced the acidity only one-third. This result, taken together with the fact that an acid soil need not contain free acid, and the further fact that forest trees do grow on acid soils, makes it plain, in the opinion of the author, that lime is valuable, not because it neutralizes acids, but because it furnishes a substance indispensable to normal plant growth. The conclusion thus reached points definitely to the use of lime as a means of combating smoke injury to vegetation and of rendering denuded areas again able to support plant life.

A supplementary investigation of the effect of metallic poisons in the soil showed that the sensitiveness of plants to these poisons varies greatly. It was found possible to arrange a complete series, leading from those which were seriously affected to those whose growth was definitely improved.—D. H. Rose.

The living plant

It is with some interest that plant physiologists and ecologists will read Ganong's[1] new book on *The living plant*. It is the first attempt in English to bring, in a comprehensive way, the main findings of these subjects within reach of the layman. The aims of the volume are well stated in the first paragraph of the preface: "It is not designed as a digest of our present scientific knowledge of plant physiology for the use of experts in the subject, but, in conformity with the aim of the series of which it is a part, it seeks to present to all who have interest to learn an accurate and vivid conception of the principal things in plant life. I was once myself such a learner, and I have tried to write such a book as I would then have delighted to read. It is, in a word, an attempt at that literature of interpretation which was forshadowed by Francis Bacon in the fine passage that stands on its dedicatory page."

Aside from the general interest in plants, we have at present a rapidly growing interest in agriculture. This makes the issue of the present clear statement of the principles of plant production especially timely. In this work the author has lived up to his high reputation as a teacher. One is surprised at the clearness and vividness with which he sets forth the main features of plant activity. Aside from presenting the main findings of the subject, the author gives a clear insight into the scientific method in action, for repeatedly he shows the processes by which the conclusions have been reached. He likewise makes clear the large cosmic relations of the subject.

[1] Ganong, William F., The living plant. 8vo. pp. xii+148. *figs. 178*. New York: Henry Holt & Co. 1913.

Citation of a few of the 18 chapter headings will give an idea of the scope and perhaps the viewpoint of the work: (i) "The various ways in which plants appeal to the interests and mind of man"; (ii) "The prevalence of green color in plants, and the reason why it exists"; (iii) "The profound effect on the structure of plants produced by the need of exposure to light"; (iv) "The kinds of work that are done by plants, and the source of their power to do it"; (xii) "The many remarkable arrangements by which plants secure union of the sexes"; (xvii) "The remarkable improvement made in plants by man, and the way he brings it about."

The author pronounces himself a vitalist of a worthy type, "perfectly natural vitalism based on the superior interpretive power of an hypothesis assuming the existence in nature of an *X*-entity, additional to matter and energy, but of the same cosmic rank as they." This is contrasted with "a supernatural vitalism of the theological type." One wonders whether the *X*-entity as defined above would not satisfy any of our present theologians, and whether the distinction is not a matter of words rather than a real difference. It should be stated that the *X*-entity is called in here only to explain the mechanics of development and inheritance. As a matter of fact, the safe position here is that of the agnostic; for we certainly do not know, in spite of assumption and positive statement to the contrary. Nor should we be discouraged by the fact that we have not made great progress in the physico-chemical explanation of development and inheritance, for the fundamental physics and chemistry of the material here involved are little developed. The serious study of the chemistry of proteins has nearly all been within the last two decades, and that of the physics of colloids within a decade. Every treatise on these subjects points out much more that is unknown than is known. The strides we are making in these fields, along with a phase of work that is now only beginning, namely, application of the methods of protein and colloidal physics and chemistry to the study of protoplasm, promise great progress in the immediate future. Here also we should not lose sight of the great contribution of KLEBS and other experimental morphologists. These are the days of hopeful agnosticism in physiology.

One is disappointed at the overworking of adaptation in the book. An adaptational explanation is apparently placed coordinate with the physical or chemical explanation. This may make the book attractive to laymen, but it hardly expresses the present spirit of plant physiology. The book also contains many statements not abreast of our present knowledge. The following sentence savors of INGENHOUSS' original statement: "It vitiates the air by its respiration, but in the long run purifies it still more by its photosynthesis." I believe it is now fully proved that vitiated air does not result from increased carbon dioxide content. Alcoholic fermentation of the yeast is spoken of as giving a copious release of energy available for growth. Also the yeast is said to be unable to respire in any other way. Per weight of sugar used, alcoholic fermentation releases about one-twentieth the energy released by aerobic

respiration, and growth does not generally occur in the yeasts in absence of aerobic respiration. One is also surprised at the author's slighting remark concerning the study of other products of alcoholic fermentation aside from carbon dioxide and alcohol, especially when he calls to mind EHRLICH'S recent important contribution on this point.—WILLIAM CROCKER.

NOTES FOR STUDENTS

Current taxonomic literature.—O. AMES (Philip. Jour. Sci. Bot. **7**:125–143. 1912), in continuation of his studies on Philippine orchids, lists 54 species of the genus *Bulbophyllum*, 19 of which are new to science.—A. BERGER (Monats. für Kakteenk. **22**:147, 148. 1912) has published a new species of *Opuntia* (*O. tomentella*) endemic in Guatemala.—A. D. BETTS (Ann. Bot. **26**:795–799. *pls. 75, 76.* 1912) describes and illustrates a new genus and species of bee-hive fungus (*Pericystis alvei*). The fungus grows on the pollen stored in the honeycomb.—E. P. BICKNELL (Bull. Torr. Bot. Club **39**:415–428. 1912) in a tenth article on "The ferns and flowering plants of Nantucket" records further data concerning the Nantucket flora and describes two new species (*Linum intercursum* and *Ilex fastigiata*).—G. BITTER (Rep. Nov. Sp. **11**:1–18, 202–237, 349–394. 1912) in continuation of his studies in the Solanaceae has published several new species and varieties from Central and South America.—F. BÖDEKER (Monats. für Kakteenk. **22**:152–155. 1912) describes and illustrates a new species of *Mamillaria* (*M. Verhaertiana*) probably indigenous in Mexico.—J. BROADHURST (Bull. Torr. Bot. Club **39**:357–385. *pls. 26–29.* 1912) in continuation of her studies in the genus *Struthiopteris* records 15 additional species, 3 of which are new to science, the others being transfers from *Lomaria* or *Blechnum*.—N. E. BROWN (Kew Bull. 281. 1912) describes a new genus (*Thorncroftia*) of the Labiatae from South Africa.—E. CHIOVENDA (Ann. di Botanica **10**:383–415. 1912) under the title "Plantae novae vel minus notae e regione aethiopica" has published several species of flowering plants new to science and proposes the following new genera: *Spathulopetalum* of the Asclepiadaceae and *Negria* of the Gramineae.—T. D. A. COCKERELL (Torreya **12**:244–247. 1912) in an article entitled "*Tragopogon* in Colorado" finds four recognizably distinct forms of this genus in Colorado, including a new hybrid (*T. porrifolius*×*dubius*).—W. G. CRAIB (Kew Bull. 266. 1912) describes a new genus (*Murtonia*) of the Leguminosae from Siam.—E. L. EKMAN (Arkiv für Botanik **11**, no. 4. pp. 61. *pls. 1–4.* 1912) under the title "Beiträge zur Gramineenflora von Misiones" includes 5 new species of grasses from Argentina.—F. FEDDE (Rep. Nov. Sp. **11**:196, 197. 1912) describes 2 new species of *Corydalis* from western North America.—M. L. FERNALD (Rhodora **14**:188–190. 1912) discusses the inland loose-flowered roseate form of "hardhack" and designates it as *Spiraea tomentosa* var. *rosea* (Raf.) Fern.; the same author (*ibid.* 192) also characterizes a hitherto unrecorded form of ash, namely *Fraxinus americana f. iodocarpa* Fern.—L. N. GOODDING (Muhlenbergia **8**:92–94. 1912) under the title "New southwestern ferns" describes 5 new species and one variety from Arizona, New Mexico, and

Sonora.—E. L. GREENE (Leaf. Bot. Obs. and Crit. **2**:229–275. 1912) has described 63 new species of flowering plants, chiefly from western North America; these pages with title-page and index close the second volume. The same author (Rep. Nov. Sp. **11**:108–111. 1912) under the heading "Novitates Boreali-Americanae VI" has published 7 new species in the genus *Cercis* from the southern and western states, and (Am. Mid. Nat. **2**:290–296. 1912) under the title "Western meadow rues I" describes 7 new species of the genus *Thalictrum*, and also (Muhlenbergia **8**:117–119. 1912) records 5 new species of *Lupinus* from Oregon and California.—J. M. GREENMAN (Field Mus. Nat. Hist. Bot. Ser. **2**:323–350. 1912) has published about 40 new species and varieties of spermatophytes, mainly from Mexico and the West Indies. One new genus (*Shafera*) of the Compositae from Cuba is included.—E. HACKEL (Rep. Nov. Sp. **11**:18–30. 1912) has published 14 new species and several varieties of grasses, mainly from Bolivia, based on the collections of Dr. O. BUCHTIEN.—E. HASSLER (*ibid.* 165–178) has published new species and varieties of Compositae and Aristolochiaceae from Paraguay.—A. A. HELLER (Muhlenbergia **8**:85–91, 103–107, 109–116. *pls. 11, 12.* 1912) describes 7 new species of *Lupinus* and (*ibid.* 132) a new *Mimulus* (*M. micranthus*) from the Pacific coast region.—F. T. HUBBARD (Rhodora **14**:165–173, 184–188. 1912) writing on "Nomenclatorial changes in Gramineae" calls attention to the names applied to certain species of grasses in the seventh edition of GRAY'S *Manual* as being at variance with the International rules of botanical nomenclature. The corrections number seventeen, and five of these are new combinations; the changes effected are mostly in the genus *Panicum*.—C. LAUTERBACH (Bot. Jahrb. **49**:1–169. 1912) in cooperation with several specialists under the title "Beiträge zur Flora von Papuasien I" has published the first of a proposed series of articles dealing with the flora of New Guinea. The present article contains descriptions of upward of 125 species and varieties new to science, and the following new genera are proposed: *Andruris* of the Triuridaceae, *Papualthia*, *Oncodostigma*, *Oreomitra*, and *Schefferomitra* of the Anonaceae.—H. LÉVEILLÉ (Bull. Géogr. Bot. **22**, IV, 217–224. 1912) gives a synoptical revision of the genus *Circaea*, recognizing 5 species, and several varieties and forms. The same author (Rep. Nov. Sp. **11**:63–67. 1912) under the title "Decades plantarum novarum" has published several new species of flowering plants from Asia and includes a new genus (*Cavaleriea*) of the Hamamelidaceae.—F. L. LEWTON (Smiths. Misc. Coll. **60**, no. 4. pp. 1, 2. *pls. 1, 2.* 1912) describes a new species of *Gossypium* (*G. irenaeum*) from Guatemala. The same author (*ibid.*, no. 5, pp. 1–4. *pls. 1–5*) proposes a new genus (*Kokia*) of the Malvaceae, and (*ibid.*, no. 6. pp. 1–10. *pls. 1–5*) records a new species of *Gossypium* (*G. Hopi*), the cotton of the Hopi Indians.—G. LINDAU (Rep. Nov. Sp. **11**:122–124. 1912) in an article entitled "Einige neue Acanthaceen" describes 3 new species in this family from Panama.—A. LINGELSHEIM (Mitteil. Thür. Bot. Ver. **29**:48, 49. 1912) has published a new species of *Acalypha* (*A. striolata*) from Brazil.—T.

LOESENER (Verhdl. Bot. Ver. Prov. Brdbg. **53**:50–86 [215–251]. 1912) in a seventh article on "Plantae Selerianae" continues the enumeration of plants collected in Mexico and Central America by C. and E. SELER. Several species and varieties new to science are included.—W. H. LONG (Mycologia **4**:282–284. 1912) describes a new species of rust (*Peridermium inconspicuum*) found on *Pinus virginiana* at Glen Echo, Maryland, and records a new generic type (*Tricella*) collected on *Coursetia glandulosa* Gray in Sabina Canyon, Santa Catalina Mountains, Arizona.—J. LUNELL (Am. Mid. Nat. **2**:287–290, 301, 302. 1912) describes 3 new species and 2 varieties of flowering plants from North Dakota.—E. D. MERRILL (Philip. Jour. Sci. Bot. **7**:227–251. 1912) under "Nomenclaturial and systematic notes on the flora of Manila" records important data concerning the flora of the Philippines and describes 6 species new to science.—J. A. NIEUWLAND (Am. Mid. Nat. **2**:299, 300. 1912) proposes the establishment of the Rafinesquean names *Agaloma* and *Lepadena* and transfers thereto several species hitherto passed by most authors as members of the genus *Euphorbia*.—C. H. PECK (N.Y. State Mus. Bull. **157**:5–139. *pls. 124–130.* 1912) in the "Report of the state botanist for 1911" under different subheadings records important data concerning particularly the fungus flora of New York and includes descriptions of about 50 new species and varieties of flowering plants.—J. PERKINS (Bot. Jahrb. **49**:170–176. 1912) in cooperation with noted specialists has published the first part of a paper on "Beiträge zur Flora von Bolivia." Descriptions of 6 new species of mosses are included.—A. PULLE (Recueil. Trav. Bot. Néerl. **9**:125–169. *pls. 2, 3.* 1912) under the title "Neue Beiträge zur Flora Surinams III" in cooperation with specialists has published several new species of flowering plants from South America. One new genus (*Clavapetalum*) of the Icacinaceae is included.—J. A. PURPUS (Monats. für Kakteenk. **22**:148–150, 161–164. 1912) in continuation of his work on the Cactaceae has published 7 new species from Mexico.—A. PUTTEMANS (Bull. Soc. Roy. Bot. Belg. **48**:235–247. 1912) in an article entitled "Nouvelles maladies de plantes cultivées" has described new species of fungi (*Oidium Begoniae*) found on leaves of *Begonia*, and *Cercospora Chrysanthemi* on leaves of *Chrysanthemum;* both host plants were in cultivation near Rio de Janeiro, Brazil.—C. R. W. K. VAN ALDERVERELT VAN ROSENBURG (Bull. Jard. Bot. Buit. Ser. II, 1–41. *pls. 1–5.* 1912) on "New or interesting Malayan ferns 4" describes several new species and proposes a new genus, namely *Scleroglossum*.—E. ROSENSTOCK (Rep. Nov. Sp. **11**:53–60. 1912) has published 12 new species and 9 varieties of ferns, based on collections made in Bolivia by Dr. O. BUCHTIEN.—H. H. RUSBY (Bull. N.Y. Bot. Gard. **8**:89–135. 1912) in a second paper on "New species from Bolivia collected by R. S. WILLIAMS" describes 113 species as new to science.—P. A. RYDBERG (Bull. Torr. Bot. Club **39**:301–328. 1912) under "Studies on the Rocky Mountain flora XXVII" describes about 30 new species of flowering plants and makes several new combinations.—W. E. SAFFORD (*ibid.* 501–508) under the title

"Desmos the proper generic name for the so-called Unonas of the Old World" revives the name *Desmos* of LOUREIRO and refers thereto 16 species, all of Old World distribution.—J. H. SCHAFFNER (Ohio Nat. **13**:19–21. 1912) records a new species of *Equisetum* (*E. kansanum*) from Kansas.—L. SCHKORBATOW (Ber. Deutsch. Bot. Gesells. **30**:474–482. 1912) under the title "Zur Morphologie und Farbstoffbildung bei einem neuen Hyphomyceten" describes a new genus and species of fungus, namely *Gemmophora purpurascens* obtained from laboratory cultures.—R. SCHLECHTER (Orchis **6**:112–119. *pls. 25–26.* 1912) has published several new species of orchids, including 4 from South America. The same author (Rep. Sp. Nov. **11**:41–47. 1912) records further new species in this family and proposes a new genus (*Xerorchis*) from Brazil, and (*ibid.* 147–150) reestablishes the generic name *Aa* Rchb. f. and refers thereto 15 species of South American orchids which have passed hitherto under *Altensteinia*.—W. A. SETCHELL (Univ. of Calif. Publ. Bot. **4**:229–268. *pls. 25–31.* 1912) under the title "Algae novae et minus cognitae I" discusses 14 species, proposing 4 new combinations, 8 new species, and 3 new genera (*Hapterophycus* in Ralfsiaceae, *Besa* in Gigartinaceae, and *Baylesia* in Dumontiaceae).—C. SKOTTSBERG (Bot. Jahrb. **48**:Beibl. 107. pp. 17–26. 1912) has published a new species of *Tetrachondra* (*T. patagonica*) from Patagonia. Hitherto the genus has been considered monotypic, occurring only in New Zealand.—O. STAPF (Kew Bull. 278. 1912) has published a new genus (*Farquharia*) of the Apocynaceae from tropical Africa.—J. STUCHLIK (Rep. Nov. Sp. **11**:151–162. 1912) under the title "Zur Synonymik der Gattung *Gomphrena* II" has published several new species and varieties of this genus from Mexico and South America.—R. THAXTER (Proc. Am. Acad. Arts and Sci. **48**:155–223. 1912) in a paper entitled "New or critical Laboulbeniaceae from Argentina" describes nearly 70 species new to science and proposes the following new genera: *Mimeomyces*, *Tetrandromyces*, *Autophagomyces*, *Cryptandromyces*, *Synandromyces*, *Zeugandromyces*, *Scaphidiomyces*, *Scelophoromyces*, and *Synaptomyces*. The same author (*ibid.* 365–386) under "Preliminary descriptions of new species of *Rickia* and *Trenomyces*" has described 18 new species of the former genus and 4 of the latter.—I. TIDESTROM (Proc. Biol. Soc. Wash. **26**:13. 1913) has published a new species of *Salicornia* (*S. utahensis*) from Toele Valley, Utah.—P. VUILLEMIN (Bull. Soc. Bot. Fr. IV. **12**:34–40. *pl. 1.* 1912) describes and illustrates a new genus (*Beauveria*) of the Verticilliaceae, based on *Botrytis Bassiana* Balsamo.—C. WARNSTORF (Philip. Jour. Sci. Bot. **7**:253–258. 1912) contributes an article on "Die Sphagna der Philippinen" and adds a new species of this genus from the Island of Luzon.—H. F. WERNHAM (Jour. Bot. **50**:241–244. *pls. 520, 521.* 1912) under the title "New Rubiaceae from tropical America I" has published several species new to science and proposes two new genera, namely *Carmenocania* and *Pseudohamelia* from Colombia and Ecuador.—G. S. WEST (*ibid.* 321–331), in continuation of his studies in the algae, records important data and proposes a new genus (*Scourfieldia*) of the Volvocaceae from Essex, England.—J. M. GREENMAN.

General biology of rusts.—Of more than ordinary biological interest is a paper by TISCHLER[3] on the relation between *Uromyces Pisi* and its aecidial host, *Euphorbia Cyparissias*. As is well known, the infection of *E. Cyparissias* by that rust takes place in the buds of the subterranean shoots in which the mycelium persists during the winter. The shoots which arise from such infected buds in the following spring show the characteristic deformations caused by the rust, but occasionally shoots are observed which outgrow the disease and develop normal leaves on their upper portion. This behavior led TISCHLER to investigate at what stage in their transition from embryonic to mature tissue the cells are subject to the formative influence of the fungus, and also to what extent such influence reaches beyond the area actually invaded by the mycelium. He found that the growing points of infected plants could be freed from the fungus by keeping the plants at a high temperature or under other conditions favoring rapid development. Under such conditions the newly developed parts of the shoots are normal. The emancipation of the growing apex from the fungus succeeds more readily as the fungus approaches the fruiting stage, and after the aecidia are mature normal branches frequently develop from the infected plants if they retain sufficient vitality. Conversely, when the formation of aecidia is suppressed (by keeping the plants in the dark), it is not possible to free the shoots from the fungus. The fungus appears to be incapable of further development after it has reached the fruiting stage.

These experiments show that the meristematic tissue of the growing point is not subject to the formative influence of the fungus, but that such influence must be exerted on cells which are no longer embryonic; nevertheless a histological examination shows that the mycelium is present even among the outer layers of embryonic cells. Here, however, the mycelium is entirely intercellular, no haustoria being formed. As soon as the cells lose their strictly embryonic character, that is, as soon as vacuoles appear in them, haustoria begin to develop from the mycelium in their intercellular spaces. The formative influence of the fungus, therefore, appears to be coincident with the formation of haustoria. The development of haustoria the author associates with the formation of soluble carbohydrates whose presence can be shown in t e older but not in the embryonic cells. The presence of hyphae among the embryonic cells shows that the growing point is not protected from invasion by substances toxic to the fungus.

Regarding the general development of the fungus, the author finds that in the rapidly growing shoots the hyphae advance in the tracheae, by means of which the fungus is enabled to keep pace with the growth of the plant. From the tracheae the infecting hyphae enter the parenchymatous tissue of the cortex, pith, and leaves. The cambium, like the embryonic cells of the growing point, is not infected. The formative influence of the mycelium on

[3] TISCHLER, G., Untersuchungen über die Beeinflussung der *Euphorbia Cyparissias* durch *Uromyces Pisi*. Flora **104**:1–64. *figs. 26.* 1911.

the stems is slight, but in the leaves the cells undergo more active divisions than those of normal leaves, and the intercellular system is more developed. These changes seem to be characteristic of the fungus, but most of the other morphological changes associated with it can also be induced by other conditions. Both in the stem and in the leaves the localization of the mycelium is dependent upon the presence of soluble carbohydrates in the tissues.

In the later stages of development of the plant, processes of disorganization begin. The death of the leaf cells is accompanied by processes characteristic of cells which are being slowly poisoned. Of the parts of the fungus the haustoria are the most persistent. In the rhizomes they become greatly developed and form a sort of pseudo-parenchymatous tissue in the cells, but they are not the sources of infection in the following year.

Of interest in connection with a consideration of the relations between parasitic fungi and their hosts are the experiments of MORGENTHALER[4] showing that the production of teleutospores is determined more by the state or condition of the host than by the influence of external factors. The author investigated the factors influencing the production of teleutospores of *Uromyces Veratri* on *Veratrum album*. He found that cutting the veins of leaves or wounding the leaves in other ways led to a production of teleutospores in the neighborhood of the wounded tissue, while in the other areas of the leaf uredospores predominated. In general, any cause that affects the leaf unfavorably leads to the production of teleutospores. In standing plants teleutospores are first formed on the lower leaves because these lose their vitality first; but if the plants are cut and kept in water, the upper leaves wilt and become discolored first. In that case teleutospores appear on the upper leaves first, even if all have been inoculated at the same time. From a number of such experiments the author concludes that the production of teleutospores is determined by the changes leading to the withering or dying of the infected parts of the host plants. This conclusion is further strengthened by a number of observations on the distribution of uredospores and teleutospores in relation to the state of the infected parts of the host in herbarium material.

KUSANO[5] gives an account of chloranthic deformation of the flowers of *Prunus Mume* caused by the mycelium of *Caeoma Makinoi*. As a result of the action of the mycelium of this fungus on the primordia of the floral parts, the course of their development is changed so that leaflike structures are produced in place of floral organs. The degree of transformation differs in different flowers. In extreme cases the cuplike receptacle bears a tuft of well developed leaves which in no way resemble floral organs. In other cases leaves take the place of only one or more of the whorls of floral organs, or some of the

[4] MORGENTHALER, O., Über die Bedingungen der Teleutosporenbildung bei den Uredineen. Centralbl. Bakt. II. **27**:73–92. *figs. 18.* 1910.

[5] KUSANO, S., On the chloranthy of *Prunus Mume* caused by *Caeoma Makinoi*. Jour. Coll. Agric. **2**:287–326. *pls. 17, 18.* 1911.

organs are only partly modified. The many resulting types are described in detail by the author. The degree of transformation is correlated with the state of development of the primordia at the time that they are infected. The influence of the fungus evidently does not extend beyond the tissue actually invaded. These conclusions, however, are drawn from observations of the visible transformations. No histological details, which would be exceedingly interesting in this case, are reported.

DIETEL[6] has published a second instalment of his studies on the factors influencing the germination of teleutospores. Among the results reported the following are of interest. The teleutospores of *Melampsora Larici-Tremulae* Kleb. are capable of germinating in March and later. Their germination takes place readily at temperatures between 8° C. and 26° C. In the study of *Puccinia graminis* Pers., it was found that the abnormal mode of germination, sometimes observed in teleutospores of this species, is determined by the temperature. At temperatures below 23° C. normal germination takes place, but at higher temperatures the teleutospores simply produce long germ tubes which occasionally become segmented. A similar mode of germination of the teleutospores of *P. Malvacearum* has been observed by TAUBENHAUS[7] and also by ERICKSSON,[7] who attributes to the "conidia" abjointed by the segmentation of the germ tube a special function in the biology of this rust. DIETEL finds, however, that in *P. Malvacearum* the formation of sporidia, or of germ tubes which segment into "conidia," is determined by the conditions under which germination takes place and not by functional differentiation of the spores. High temperature and lack of moisture favor the production of abnormal germ tubes.

To the few observations which have been made on the transmission, from the stock to the scion, and inversely, of grafted plants, of qualities producing immunity from the attack of fungi to which one or the other is subject, FISCHER[8] adds a further observation supporting the general conclusion that no such mutual influence between the stock and the scion exists. He finds that plants of *Mespilus*, which cannot be infected by the basidiospores of *Gymnosporangium confusum*, remain immune even when united by grafting with susceptible species of *Crataegus*, nor is the susceptibility of the *Crataegus* changed.

A special case is presented by *Crataegomespilus Asnieresii*, which is a chimaera consisting of a *Crataegus* core with a *Mespilus* epidermis. Here FISCHER found that the germ tubes of the basidiospores penetrated the epidermis and infected the *Crataegus* tissue underneath. He reserves his opinion, however, as to any mutual influence of the two parts of the plants, stating

[6] DIETEL, P., Versuche über die Keimungsbedingungen der Teleutosporen einiger Uredineen. II. Centralbl. Bakt. II. **35**:272–285. 1912.

[7] Rev. in BOT. GAZ. **54**:431–433. 1912.

[8] FISCHER, ED., Beiträge zur Biologie der Uredineen. Mycol. Centralbl. **1**:195–198. 1912.

that it is not certain that the species of *Mespilus* entering into the foregoing chimaera is immune, and even if it were, the result of the experiment does not imply that the *Mespilus* epidermis had become susceptible, since it is known that germ tubes of fungi frequently penetrate inert membranes and even the epidermis of plants in whose tissues they are unable to make any further growth.

ORTON[9] describes a number of cases of correlation in the distribution of certain heteroecious species of *Puccinia* and *Uromyces*. The forms thus correlated have for their telial hosts the same species or closely related species of the same genus, while their aecidia occur on alternate hosts which are either identical or which are species of one genus. The aecidia and the uredospores of the associated rusts are similar in structure, form, and color, while the teleutospores differ only in number of cells. As examples may be cited *Puccinia subnitens* and *Uromyces Peckeanus*, both of which occur on *Distichlis spicata* and have aecidia similar in their essential characteristics on species of the Chenopodiaceae; also *Puccinia Caricis-Asteris* and *Uromyces perigynius* with teleutospores on species of *Carex* and aecidia on members of the Compositae. This condition appears to point to a close relationship between the two genera *Puccinia* and *Uromyces*.

In opposition to the view that rust-infected grains of cereals are the agencies by which the grain rusts are carried over from year to year, ERIKSSON[10] points out that grains bearing rust pustules are, both in his own experiments and according to statements in the literature, of very rare occurrence; and that plants developing from such grains do not become infected earlier nor more severely than plants from normal seeds. Furthermore, a cytological study of a large number of plants from plots which afterward were badly rusted failed to show the presence of mycelium by means of which the rust might have lived through the winter. He concludes, therefore, that the rust pustules on infected seed grain are of no significance in connection with the rust of the grain crop.—H. HASSELBRING.

Chloroplasts and chlorophyll.—LIEBALDT'S work[11] on chloroplasts emphasizes again the important part colloidal chemistry is coming to play in physiological problems. The chloroplast is considered a two-phase disperse system. The pigments, especially the green ones, constitute the lipoid phase, and the stroma, insoluble in lipoid solvents, coagulable with heat and alcohol, and swelling in water, is the hydroid phase. The lipoid phase shows amicronic (in particles beyond the vision of the ultramicroscope) dispersal through the

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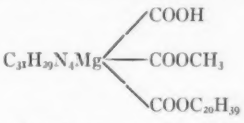
[9] ORTON, C. R., Correlation between certain species of *Puccinia* and *Uromyces*. Mycologia **4**:194–204. *pls. 2*. 1912.

[10] ERIKSSON, J., Rostige Getreidekörner- und die Überwinterung der Pilzspecies. Centralbl. Bakt. II. **32**:453–459. 1912.

[11] LIEBALDT, ERNA, Über die Wirkung wässeriger Lösung oberflächenaktiver Subitanzen auf die Chlorophyllkörner. Zeitsch. Bot. **5**:65–113. 1913.

hydroid phase, hence the chloroplast is generally homogeneous when viewed with either the microscope or the ultramicroscope. The hydroid phase of the chloroplast absorbs considerable additional water when it is brought into direct contact with this agent. This disturbs the dispersion of the two phases and the green pigment accumulates in various regions, giving the plastid a granular appearance. This, the writer believes, is not a complete separation of the two phases, for the green granules are not as dark colored as the separate drops of the pigment, and the lipoid phase will not strain with Sudan III nor the hydroid phase with neutral red, both of which occurs in a true separation of the two phases. Water solutions of various alcohols in concentrations too low to coagulate the hydroid phase hasten and accentuate the deformation caused by distilled water, but do not cause a true separation of the two phases. If the alcohol is sufficiently concentrated to coagulate the hydroid, a complete separation occurs. In this process the separation of the pigment passes from amicronic dispersal through submicronic (particles visible to the ultramicroscope but not to the microscope) and micronic (visible to the microscope) to complete separation. This work gives quite a different picture of the relation existing between stroma and pigments in the normal chloroplast from that generally depicted in texts. The texts generally speak of the pigment being held in the meshes of the spongy stroma or aggregated in the outer layers of the plastid. The author can gain either of these pictures by one or another method of deformation. He does not deny that such a deformation occasionally occurs even in the living active cell, but the chloroplast is generally homogeneous and shows amicronic distribution of the two-phase system. This agrees with the dispersal of the various phases in the protoplasm which is optically empty aside from the microns in it. Plastids of the various plant groups vary in their consistency and resistance to agents; those of the Florideae are most nearly liquid.

By use of alcohols as solvents, the author was able to obtain crystals of the green pigments from many green plants, ranging from the algae up. The form and structure of the crystals vary with the alcohol used. The advance of our knowledge of the chemistry of chlorophyll during the last half-decade enables us to state with reasonable certainty the general constitution of the green pigments as they exist in the plastid, also of the crystalline products in methyl and ethyl alcohol. TSWETT's contention that there are two green pigments (termed by him α and β chlorophyllin) has been confirmed by WILLSTÄTTER, who has shown that they are different oxidation stages of the same substance. According to this writer one of them can be represented as follows:



The molecule bears three carboxyl groups. One is free, another bears a methyl group, and the third a phytol group. In extraction with ethyl alcohol the

phytol group is displaced by the ethyl group and the ethyl derivatives crystallize out. With methyl alcohol the crystals are the methyl derivatives. WILLSTÄTTER speaks of the native green pigments as phytylchlorophillids. On the same basis the ethyl derivatives are ethylchlorophillids. The displacement of the phytol by the ethyl group is hastened by an esterase (chlorophyllase). The phytyl derivatives are amorphous, while the ethyl and methyl derivatives are crystalline. The constitution of the green crystals given with ketones, esters, and aldehydes is unknown.—WM. CROCKER.

Silver leaf.—Güssow[12] reports that the peculiar disease known as "silver leaf" is common on fruit trees in Canada. This disease has been recognized and has received distinctive names in several European countries. Its chief symptom, as its name indicates, is a silvery appearance of the leaves which is brought about by the separation of the epidermis from the palisade cells and the consequent filling of the resulting space with air. The wood of the diseased trees is browned and contains mycelium. After the death of the affected trees, fruit bodies of *Stereum purpureum* develop on the trunks and branches. This fungus has been shown by PERCIVAL, PICKERING, and others to be causally associated with the disease. The observations of these investigators are confirmed by GÜSSOW's experiments in Canada, where in many cases he was able to produce the disease in 100 per cent of the inoculated trees. He also found that scions grafted on diseased trees soon became infected. In all cases the wood is infected with the mycelium of *Stereum purpureum*, but the most striking feature of the disease is the total absence of the mycelium from the diseased leaves. The mode in which the separation of the epidermis from the underlying tissue is brought about by the fungus was not determined. The disease appears to furnish an example of physiological effects wrought by the action of the mycelium on parts of the host not actually invaded. Such phenomena, where the effects cannot be traced to mere mechanical injury, are practically unknown in the field of plant pathology.—H. HASSELBRING.

Cytology of Laboulbeniales.—As a sequence to his general introductory account[13] of the cytology of the Laboulbeniales, FAUL[14] has published a full account of the special morphology of two species, *Laboulbenia chaetophora* and *L. Gyrinidarum*. These two forms lack antheridia; therefore the study of them is not complicated by the question of fertilization by spermatia. The young procarp consists at first of the carpogonium, the trichophoric cell, and the trichogyne. The nucleus of the carpogonium and that of the trichophoric cell divide, and at about the same time the wall between the two cells

[12] GÜSSOW, H. T., Der Milchglanz der Obstbäume. Zeitschr. Pflanzenkrank. **22**:385–401. *figs. 1. pls. 2.* 1912.

[13] Rev. in BOT. GAZ. **54**:84. 1912.

[14] FAUL, J. H., The cytology of *Laboulbenia chaetophora* and *L. Gyrinidarum*. Ann. Botany **26**:325–355. *pls. 4.* 1912.

disappears, so that the four nuclei come to lie in a single cell. The upper and lower ends of this cell are cut off as the "restored trichophoric cell" and the inferior supporting cell. Each of these contains a single nucleus. The two remaining nuclei undergo a series of conjugate divisions, as a result of which a superior supporting cell, and sometimes a secondary inferior supporting cell, each with two nuclei, are cut off. Two nuclei, presumably one derived from each nucleus of the original pair, remain in the parent cell or ascogonium. The ascogonium may either give rise to asci directly, thus itself becoming an ascogenous cell, or it may divide and give rise to two ascogenous cells. The only nuclear fusion in the life cycle of the plant is that which takes place in the ascus.—H. HASSELBRING.

Mitochondria.—The literature on mitochondria is growing, but as it grows the difficulty in defining the structures becomes greater and greater. Just as centrosomes were followed by centrosome-like bodies and blepharoplasts by blepharoplastoids, the mitochondria are now followed by mitochondria-like structures. WOYCICKI[15] describes in the pollen mother cells and microspores of *Malva silvestris* mitochondria-like bodies, which first appear as small granules, then become vacuolate and divide by constriction, and finally disappear completely after the formation of the intine. Starch is entirely lacking during these stages, starch grains first appearing after the exine has become differentiated. The mitochondria-like bodies have nothing to do with leucoplasts or the formation of starch. In *Malva* they resemble somewhat the proteid vacuoles of Coniferales.

Improvements in technic have certainly brought to light some minute structures of the cell which were previously overlooked, but what these structures are and what their significance may be, are problems still awaiting solution.—CHARLES J. CHAMBERLAIN.

Wilting coefficient in alkali soils.—In a series of 14 alkali soils, graduated according to their salt content, KEARNEY[16] has shown the wilting coefficients to be practically identical, but the time required for the exhaustion of the water available for growth steadily increased with the increasing salt content. The plants were proportionately smaller when the wilting coefficient was reached in the soils of greater salt content, that is, the presence of alkali increased the quantity of water transpired in producing a unit weight of dry matter. With too great a quantity of salts, pathological conditions were evident in the plants and the wilting coefficient was not reached.—GEO. D. FULLER.

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[15] WOYCICKI, Z., Über die mitochondrienänliche Gebilde in den Gonotokonten und Gonen bei *Malva silvestris* L. Sitzungsber. Warschauer Gesell. Wiss. **5**:167–182. *pls. 1, 2.* 1912.

[16] KEARNEY, THOMAS H., The wilting coefficient for plants in alkali soils. Bur. Pl. Ind. Circ. **109.** pp. 9. 1913.

Morphology of the podocarps.—SINNOTT[17] has investigated the reproductive structures of the Podocarpineae and has come to some conclusions in reference to the relationships of the group. The detailed results are too numerous to be cited here, but the author has canvassed the structures of the ovulate strobilus, the characteristic male gametophyte, the wings of the pollen grains, the female gametophyte, fertilization, the proembryo, and the endosperm, and has concluded that the group has been derived from the Abietineae through forms resembling *Podocarpus*, which is therefore the oldest genus. Some striking resemblances between the podocarps and araucarians further suggest that both of these groups may have arisen from an ancient group closely allied to the Abietineae. A connection with the taxads is also suggested by resemblances between *Cephalotaxus* and certain species of *Podocarpus*, the conclusion being that the Taxineae, through *Cephalotaxus* (its most ancient genus), may have arisen from some ancient member of the Podocarpineae.—J. M. C.

Adventive branches in Frullania.—Miss LORENZ[18] finds that 4 of the 11 species of *Frullania* in New England reproduce vegetatively by adventitious shoots. From her statements it seems that a marginal cell of a leaf enlarges; that the first two planes of division are anticlinal, giving a quadrant of more or less unequal cells; that the next plane of division is periclinal; that from one of the outer cells of the resulting octant a pyramidal apical cell which gives rise to the shoot is developed. The first leaves of the shoot are rudimentary, but very soon the adult form appears. Ventral leaves are also delayed. As should perhaps be expected, these vegetative shoots are more frequent on dioecious than on autoecious species.—W. J. G. LAND.

Origin of species in Hieracium.—OSTENFELD[19] has conducted an extensive set of experiments with *Hieracium* to discover the possible relationship between its polymorphism and its strong tendency to apogamy. He has reached the conclusion that new forms arise as hybrids and also by single variations (mutations), and that in both of these cases "the prevailing apogamy supports their existence and constancy." This means that the polymorphism of the genus is correlated with its apogamy.—J. M. C.

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[17] SINNOTT, EDMUND W., The morphology of the reproductive structures in the Podocarpineae. Ann. Botany **27**:39–82. *figs. 9. pls. 5–9.* 1913.

[18] LORENZ, ANNIE, Vegetative reproduction in the New England Frullaniae. Bull. Torr. Bot. Club **39**:279–284. *figs. 3.* 1912.

[19] OSTENFELD, C. H., Experiments on the origin of species in the genus *Hieracium* (apogamy and hybridism). New Phytol. **11**:347–354. 1912.